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Patterns of Gene Flow and Genetic Divergence in the Northeastern Pacific Clinidae (Teleostei: Blennioidei), Based on Allozyme and Morphological Data

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Genetic relationships and distribution patterns among populations, subspecies, and species of northeastern Pacific myxodin clinids were analyzed from allozyme data. The most recent revision recognized six species and 12 subspecies in two genera, *Heterostichus* and *Gibbonsia*. Allozymes from 40 gene loci from all 12 nominal taxa were analyzed to compare heterozygosity levels, Hardy-Weinberg equilibrium conformance, genetic distances, and phylogenetic relationships. Sample sites ranged from Carmel, California, to central Baja California, Mexico, and included areas of sympatry, disjunct distribution, and relative isolation. Offshore island sites included the California Channel, San Benito, and Guadalupe islands; the last with several endemic nominal taxa. In addition, morphological characters putatively defining closely related taxa were reexamined because preliminary data suggested that some taxonomic separations had been made on the basis of sexually dimorphic characters and ecophenotypic variation.

Most intraspecific samples shared close genetic relationship, consistent with little genetic isolation. Disjunct populations of *G. montereyensis* and *G. metzi* from north of Point Conception, California, and in areas of coldwater upwelling off northern Baja California, Mexico, respectively, are very similar. The Channel Island populations are little divergent from those of the mainland, however, the San Benito Islands population is slightly more genetically distinct. Populations of the geographically isolated Guadalupe Island are genetically divergent. Patterns of genetic relationships among populations may be explained by the relatively long larval life of clinids (up to two months), geographic continuity, and major coastal current patterns. Some allelic variation in *G. elegans, G. montereyensis,* and *G. metzi* also supports longitudinal clinal trends, which may suggest selection resulting from temperature.

Both allozyme and morphological data failed to separate *G. erythra* from *G. montereyensis. Gibbonsia erythra* is a deepwater ecophenotype of *G. montereyensis*; males inhabit deeper water than females, and the supposed distinguishing characters are sexually dimorphic and/or depth related. *Gibbonsia norae* is a semi-isolated population of *G. montereyensis* inhabiting the San Benito and Guadalupe islands, Mexico. A new key to the northeastern Pacific Clinidae is given.

MYXODIN clinids or kelpfishes are among the most common temperate nearshore fishes living in benthic algae along the Pacific coast of North America (Williams, 1954; Stepien, 1986a; Stepien et al., 1988). According to C. Hubbs' (1952) revision, the group comprises six species and 12 subspecies in two genera, *Heterostichus* and *Gibbonsia*. The most abundant species of northeastern Pacific myxodins have two general patterns of distribution: north (*G. metzi* and *G. montereyensis*) and south (*G. elegans* and *H. rostratus*) of Point Conception, California (34.5°N, Fig. 1). A temperature boundary at Point Conception roughly separates the northern, cold temperate Oregonian biogeographic region from the southerly warm temperate Cal-

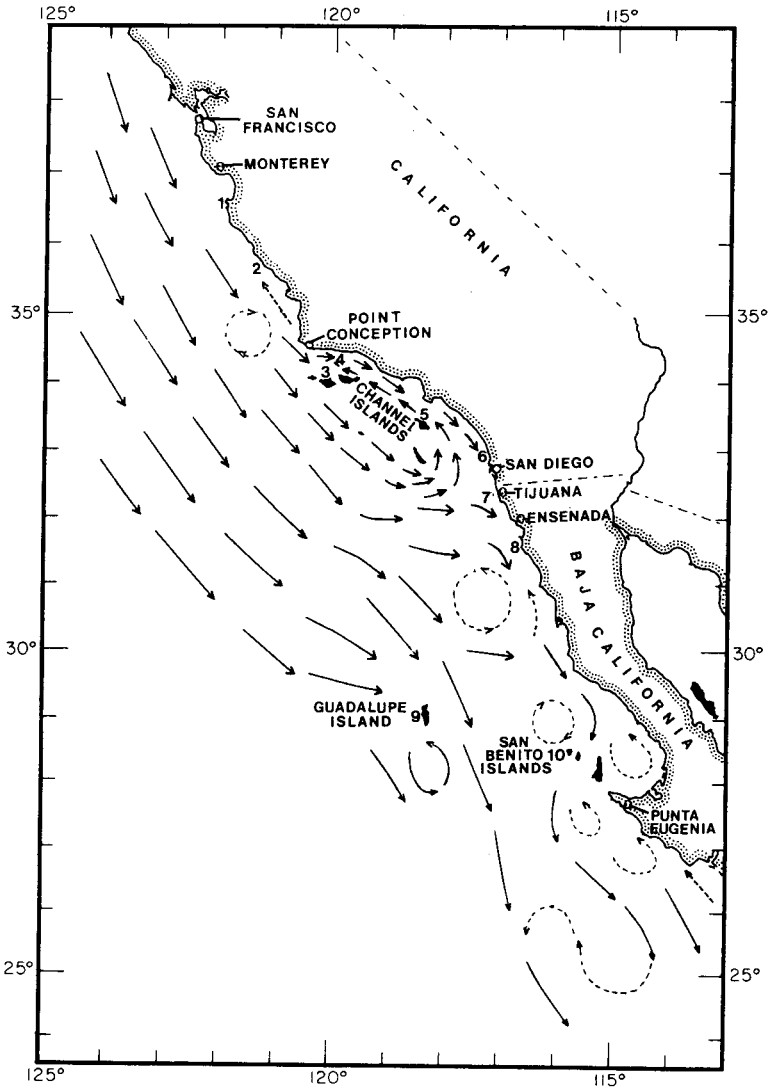

Fig. 1. Location of sample sites, numbered from north to south, as follows: 1 = Carmel, 2 = San Simeon, 3 = Santa Cruz Island, 4 = Santa Barbara, 5 = Santa Catalina Island, 6 = La Jolla (San Diego), 7 = Coronado Islands, 8 = Punta Clara, 9 = Guadalupe Island, 10 = San Benito Islands. Mean current flow patterns in the study area are represented (adapted from Waples and Rosenblatt, 1987 and based on data from Wyllie, 1966; Hickey, 1979; Owen, 1980; and Cowen, 1985). Consistent flow directions are shown with solid arrows; dashed arrows indicate more variable features.

ifornian province (Hedgpeth, 1957; Valentine, 1966; Briggs, 1974; see Table 1 for temperature comparisons). Point Conception is a distributional boundary for many other fishes (C. L. Hubbs, 1960; Horn and Allen, 1978), invertebrates (Garth, 1960; Seapy and Littler, 1980), and algae (Dawson, 1960; Abbott and Hollenberg, 1976; Murray et al., 1980).

However, some of the northern species, including the clinids *G. montereyensis* and *G. metzi*, reappear in pockets of nearshore summer cold water upwelling off Baja California, Mexico, as

TABLE 1. MEAN SEASONAL TEMPERATURES (C) NEAR SOME CLINID COLLECTION SITES, SUMMARIZED FROM CALCOFI DATA 1950–78 (LYNN ET AL., 1982).

CALCOFI station	Location	Depth (m)	Seasonal mean				Yearly mean
			Jan	Apr	July	Oct	
80052	Point Conception, California	0	13.66	11.95	12.76	16.07	13.61
	34.5°N, 120°60'W	10	13.64	11.66	12.19	15.62	13.30
		20	13.43	11.18	11.48	14.05	12.54
		30	12.21	10.66	10.82	12.73	11.85
90028	Dana Point, California	0	14.27	15.21	19.15	18.57	16.80
	33°N, 118°W	10	14.05	14.46	16.66	17.87	15.79
		20	13.93	13.23	13.57	15.66	14.10
		30	13.68	12.15	11.96	13.81	12.90
100030	Ensenada, Mexico	0	14.61	16.14	17.51	17.32	16.40
	32°N, 116°30'W	10	14.49	15.99	15.03	16.23	15.44
		20	14.24	15.09	13.33	14.42	14.27
		30	13.84	14.28	12.10	13.40	13.43
110035	Punta Baja, El Rosario, Mexico	0	15.72	14.58	16.93	18.59	16.46
	30°N, 116°W	10	15.68	14.47	16.27	18.41	16.21
		20	15.48	13.92	15.14	17.86	15.60
		30	15.27	13.34	14.06	16.52	14.80
110070	Guadalupe Island, Mexico	0	16.05	16.46	18.75	19.93	17.80
	39°N, 118°45'W	10	15.96	16.38	18.51	19.84	17.67
		20	15.85	16.28	18.17	19.79	17.52
		30	15.79	16.17	17.72	19.66	17.34
120035	San Benito Islands, Mexico	0	16.30	15.68	18.64	20.22	17.71
	28.5°N, 116°W	10	16.29	15.33	18.53	19.79	17.49
		20	16.24	15.08	18.18	19.68	17.30
		30	16.17	14.72	17.72	19.16	16.94
120045	Punta Eugenia, Mexico	0	16.67	15.45	18.40	20.60	17.78
	28°N, 115°20'W	10	16.65	15.31	18.10	20.53	17.65
		20	16.55	14.99	16.66	19.79	17.00
		30	16.44	14.22	15.42	18.13	16.05

well as in deeper waters off some of the offshore islands (C. L. Hubbs, 1952, 1960; C. Hubbs, 1952; Garth, 1960). This disjunct coastal distribution pattern, although presumably widespread (C. L. Hubbs, 1952; Dawson, 1960), has been little studied, and we do not know of other investigations that have focused on population genetics of these organisms. One of the goals of the present study was to examine the degree of genetic isolation and gene flow among clinids having this disjunct distribution pattern.

Stepien et al. (1991) recently completed a yearlong survey of fishes at one of the intertidal cold-water upwelling sites off northern Baja California (Punta Clara), where some species characteristic of both marine provinces occur sympatrically. For example, four species of clinids (*H. rostratus, G. elegans, G. metzi,* and *G. montereyensis*) were collected in the same tidepools at the Punta Clara upwelling site, which were analyzed in the present study. No other site examined had such diversity of sympatric clinids.

Waples and Rosenblatt (1987) and Waples (1986, 1987) examined gene flow among populations of eight species of warm temperate fishes having primary distributions south of Point Conception. Fishes from some of their study areas were examined in the present study so comparisons can be made. Comparisons were also made with other studies of population genetics of fishes from some of these areas, including the cottid *Clinocottus analis* (Swank, 1979), the hexagrammid *Oxylebius pictus* (Davis et al., 1981), the sciaenids *Genyonemus lineatus* and *Seriphus politus* (Beckwitt, 1983), the serranid *Paralabrax clathratus* (Beckwitt, 1983), the stichaeid *Anoplarchus purpurescens* (Sassaman et al., 1983), the atherinid *Atherinops affinis* (Crab-

TABLE 2. FORMER AND PRESENT STATUS OF THE NORTHEASTERN PACIFIC MYXODIN CLINIDAE.

Former status (C. Hubbs, 1952) and general distribution	Present status
1. *H. rostratus* Girard, 1854	1. *Heterostichus rostratus*
a. *H. r. rostratus* Girard, 1854 —Baja California to Pt. Conception	a. not recognized
b. *H. r. guadalupensis* C. Hubbs, 1952 —Guadalupe Island endemic	b. not recognized
2. *G. elegans* Cooper, 1864	2. *Gibbonsia elegans*
a. *G. e. elegans* Cooper, 1864 —Baja Calif. to Pt. Conception, intertidal	a. not recognized
b. *G. e. velifera* C. Hubbs, 1952 —Baja Calif. to Pt. Conception, offshore	b. not recognized
c. *G. e. erroli* C. Hubbs, 1952 —Guadalupe Island, endemic	c. not recognized
d. *G. e. rubrior* C. Hubbs, 1952 —Guadalupe Island, endemic	d. not recognized
3. *G. metzi* C. L. Hubbs, 1927	3. *Gibbonsia metzi*
a. *G. m. metzi* C. Hubbs, 1952 —Pt. Conception to Alaska	a. not recognized
b. *G. m. ferventer* C. Hubbs, 1952 —Baja California to Pt. Conception	b. not recognized
4. *G. montereyensis* C. L. Hubbs, 1927	4. *Gibbonsia montereyensis*
a. *G. m. montereyensis* C. L. Hubbs, 1927 —Pt. Conception to Alaska, rough water	a. not recognized
b. *G. m. vulgaris* C. Hubbs, 1952 —Pt. Conception to Alaska, calm water	b. not recognized
5. *G. erythra* C. Hubbs, 1952 —Baja California to Pt. Conception, subtidal	5. Placed in the synonymy of *G. montereyensis*
6. *G. norae* C. Hubbs, 1952 —Guadalupe and San Benito Islands, endemic	6. Placed in the synonymy of *G. montereyensis*

tree, 1986), the blenniid *Hypsoblennius jenkensi* (Present, 1987), and the girellid *Girella nigricans* (Orton, 1989).

Gene products from 40 allozyme loci of all six North American myxodin clinid species and 12 subspecies, as defined by C. Hubbs (1952), were analyzed in the present study. Sample sites ranged along the North American Pacific coast from Soberanes Point, Carmel, California, to central Baja California, Mexico, and included several of the offshore islands, e.g., the Channel, Coronado, San Benito, and Guadalupe islands (see Fig. 1). Sample sites represent both the center of the range of each species and areas of infrequent occurrence and sympatry with related species.

Guadalupe Island, the most isolated site sampled, is 275 km west of the coast of central Baja California, Mexico, and surrounded by deep (>3000 m) water (Fig. 1). Several subspecies and one species of clinid were described by C. Hubbs (1952) as endemic to Guadalupe Island (the endemic species was said to also occur at the San Benito Islands; see Table 2). At one time, Guadalupe Island was believed to have many other endemic fishes (C. L. Hubbs and Rechnitzer, 1958; C. L. Hubbs, 1960). However, more recent studies have shown that some of these have more widespread distributions (Greenfield and Wiley, 1968; Briggs, 1974), and other genetic studies have suggested substantial gene flow between some Guadalupe Island and mainland fish populations (other than clinids; Waples and Rosenblatt, 1987; Waples, 1986, 1987; Orton, 1989). An objective of the present study was to test whether, and to what degree, clinid populations from Guadalupe Island are genetically distinct.

Genetic relationships of all clinid taxa (Table 2) were analyzed in the present study, and some of their morphological characters were also reexamined. C. Hubbs (1952) divided the former *G. montereyensis* into three species, erecting *G. erythra* and *G. norae*. *Gibbonsia erythra* was sep-

arated from *G. montereyensis* on the basis of a higher anterior portion of the dorsal fin and squamation extending to the edge of the caudal peduncle (as opposed to a naked area on the peduncle, characteristic of *G. montereyensis*). Individuals identifiable as *G. erythra* are most common in deeper subtidal areas south of Point Conception, California. This complex was a particular focus of the present study because preliminary examination suggested that all *G. erythra* are males. *Gibbonsia norae,* endemic to Guadalupe and the San Benito islands, Mexico, was separated on the basis of having a smaller number of dorsal and anal-fin rays and fewer scale rows above the lateral line (C. Hubbs, 1952).

Many of the meristic characters utilized by C. Hubbs (1952) as discriminators overlap considerably among the 12 clinid taxa. In the present study, allozymes provided a data set that was analyzed separately from morphological data to test patterns of relationships and the delineation of taxa. In addition, life-history and ecological data for *H. rostratus* (Stepien, 1986a, 1986b, 1987) and *G. elegans* (Williams, 1954; Stepien et al., 1988) showed that sexual dimorphism is common in this group and suggested that some subspecies were defined on the basis of sexually dimorphic and depth-related characters. Sexes of North American clinids are depth segregated; adult males are usually found deeper than adult females and juveniles (Williams, 1954; Stepien, 1986a, 1987; Stepien et al., 1988), so that single collections are almost always skewed in sex ratio. The deep-versus-shallow subspecies pairs described by C. Hubbs (1952) were, thus, reexamined for sexually dimorphic and depth-related morphological variation, as well as tested for genetic divergence.

Materials and Methods

Species and locations analyzed.—Allozyme data from all species (*H. rostratus, G. elegans, G. metzi, G. montereyensis, G. erythra,* and *G. norae*) and subspecies of North American myxodins, comprising all 12 taxa recognized by C. Hubbs (1952), were analyzed. Our 10 collection localities and general distribution patterns are given in Figure 1 and Table 2, respectively. Specimens were collected by netting intertidally with use of the anesthetic quinaldine or subtidally by scuba diving and were immediately frozen and stored at −40 C. Voucher specimens of representatives from all sites were deposited in the Scripps Institution of Oceanography (SIO) Marine Vertebrates Collection.

Approximately equal numbers of females and males were analyzed for all populations sampled, excepting *G. erythra* (all males). Sexing was based on examination of whole gonads or gonadal tissue, using a dissection microscope. Gonadal maturities were ranked from 1 to 5, following Stepien (1986a), 1 being immature and 5 being ripe. Separation of individuals of *G. erythra* from *G. montereyensis* fit C. Hubbs' (1952) criterion based on degree of squamation on the caudal peduncle and ratio of the height of the first dorsal spine (SH) to head length (HL).

To investigate sexual dimorphism, scale patterns on the caudal peduncle of *G. montereyensis* and *G. erythra* were ranked from 1 to 5, according to increasing degree of scale coverage. Variation of these scale patterns among males and females was tested with chi-square tests (Sokal and Rohlf, 1981). The SH, HL, standard length (SL), and total length (TL) were measured, following the methods of C. Hubbs (1952), using a dissection microscope, for a series of collections of *G. montereyensis* and *G. erythra* from known depths. In addition, comparisons of measurements of caudal peduncle length (PL) : HL and SL and SH : HL and SL were made for *G. elegans erroli* and *G. elegans rubrior* of known depths from Guadalupe Island. All measurements were taken prior to sexing.

Enzyme electrophoresis.—Separate extracts of eye, liver, and muscle were prepared from each specimen. Tissues were homogenized in a 1:1 volume : volume mixture of tissue and 0.1 M potassium phosphate grinding buffer (pH 7; Waples and Rosenblatt, 1987) and centrifuged at 20,000 *g* for 10 min. The supernatant fraction was then subjected to horizontal starch electrophoresis in 12.5% starch gels (Sigma starch; Sigma Chemical Co., St. Louis, Missouri 63178). The enzymes and tissues surveyed, loci scored, and buffer solutions used are listed in Table 3. Staining methods and recipes were adapted from Selander et al., 1971; Waples, 1986; and Buth and Murphy, 1990. Enzyme nomenclature follows recommendations of the International Union of Biochemistry (1984). Alleles are designated with lowercase letters.

Only 34 loci from the Guadalupe Island population of *H. rostratus* and loci from the Guadalupe Island population of *G. elegans* are included because these samples were previously analyzed by Waples (1986), who contributed tis-

TABLE 3. LIST OF ENZYMES SURVEYED IN ELECTROPHORETIC ANALYSES.

Name (E.C. number)	Locus	Tissue*	Buffer**
Acid phosphatase (3.1.3.2)	Acp-1	L	1
	Acp-A	L	1
Aconitase hydratase (4.2.1.3)	Acoh-A	L	1
Adenylate kinase (2.7.4.3)	Ak-A	M	1, 2
Alcohol dehydrogenase (1.1.1.1)	Adh-A	L	2, 3
	Adh-B	L	2, 3
Aspartate aminotransferase (2.6.1.1)	sAat-B	L	1, 2
	sAat-A	M	1, 2
	mAat-A	L, M	1, 2
Creatine kinase (2.7.3.2)	Ck-B	E	2
	Ck-C	L	1, 2
	Ck-A	M	1, 2
Esterase (3.1.1.–)	Est-1	L, M	4
	Est-2	L, M	4
	Est-3	L, M	4
Fumarate hydratase (4.2.1.2)	Fumh-A	L	1, 2
Glucose–6–phosphate dehydrogenase (1.1.1.49)	G6pdh-1	L	2, 3
	G6pdh-2	L	2, 3
Glucose-6-phosphate isomerase (5.3.1.9)	Gpi-A	E, L, M	2, 4
	Gpi-B	M, E	2, 4
Glutamate dehydrogenase (1.4.1.2)	Gtdh-A	L, M	1
Glyceraldehyde–3–phosphate dehydrogenase (1.2.1.12)	Gapdh-C	E, L	1, 2
	Gapdh-A	M	1, 2
Glycerol–3–phosphate dehydrogenase (1.1.1.8)	G3pdh-B	L, M	1, 2
L-Iditol dehydrogenase (1.1.1.14)	Iddh-A	L	1
Isocitrate dehydrogenase (NADP) (1.1.1.42)	sIdh-A	E, L	1, 2
	mIdh-A	E, M	1, 2
L-Lactate dehydrogenase (1.1.1.27)	Ldh-C	E	1, 2
	Ldh-A	E, M	1, 2
	Ldh-B	E, L	1, 2
Malate dehydrogenase (1.1.1.37)	sMdh-B	M	1, 2
	sMdh-A	L	1, 2
Mannose–6–phosphate isomerase (5.3.1.8)	Mpi-A	L, M	2
Phosphoglucomutase (5.4.2.2)	Pgm-A	L, M	1, 2
Phosphogluconate dehydrogenase (1.1.1.44)	Pgdh-A	M	1
Peptidase (glycyl-l-leucine) (3.4.11.–)	Pep-A	L, M	4
Peptidase (l-leucylglycylglycine) (3.4.11.–)	Pep-B	L, M	4
	Pep-3	L, M	4
Superoxide dismutase (1.15.1.1)	sSod-A	L	3
Xanthine dehydrogenase (1.1.1.204)	Xdh-A	L	1, 3

* Tissues: L = liver, M = muscle, E = eye (retina).
** Buffers: 1 = Tris-citric acid pH 6.9, 2 = Tris-citric acid pH 8.0, 3 = Tris-boric acid EDTA pH 8.6, 4 = Lithium hydroxide (recipes adapted from Selander et al., 1971; Shaklee et al., 1982; Waples, 1986; and Buth and Murphy, 1990).

sue samples, fixed gels, and original scored data to this study. Condition of this frozen material precluded further electrophoretic work and fresh samples from Guadalupe Island could not be obtained. Gene products in these Guadalupe Island samples included all of the polymorphic loci determined in the other populations of *Heterostichus* and *G. elegans*. Loci examined included all listed in Table 3 except Acp-1, Est-1, G6pdh-2, Iddh-A, Mpi-A, and Xdh-A for *H. rostratus* and Aat-A, Acp-1, Ck-C, Est-1, Est-2, Gapdh-C, G6pdh-1, G6pdh-2, and Iddh-A for *G. elegans*. All gels and original data were reexamined; and stains, buffers, and scoring corresponded to those used by Waples (1986).

Data analysis.—BIOSYS–1 vers. 1.7 (Swofford and Selander, 1981, 1989) was used to compute

measures of genetic variability (heterozygosity, number of polymorphic loci, and F-statistics; Wright, 1965, 1978), to quantify divergence among the geographic samples (contingency table analyses of heterogeneity among populations), to test conformance with Hardy-Weinberg equilibrium expectations (with Levene's, 1949 correction for small samples), and to calculate Nei's (1972) and modified Rogers' (Rogers, 1972; Wright, 1978) genetic distances between all pairwise combinations of taxa. This program was also used to construct distance Wagner trees (Farris, 1972), using modified Rogers' genetic distances (Wright, 1978).

Allozyme data for *G. elegans* from Bird Rock, California, were compared with data collected by R. Waples (1982 collection unpubl.) using chi-square contingency analyses (Sokal and Rohlf, 1981), to test for temporal variation in allelic frequencies. Collections of *G. elegans, G. metzi, G. montereyensis,* and *H. rostratus* made in 1986–87 and 1987–88 from San Simeon, La Jolla, California, and Punta Clara, Mexico, were also analyzed for temporal variation.

All statistical tests and distance clustering analyses were performed twice in the present study, with the full data set of 40 loci for all populations except Guadalupe Island and again with the data set of 31 loci for all populations of *Heterostichus* and *G. elegans.* Analyses of morphological data (chi-square contingency and regression tests) were performed using SYSTAT (Wilkinson, 1988).

Results

Genotypic data for all polymorphic loci of *H. rostratus, G. elegans, G. metzi, G. montereyensis, G. erythra* and *G. norae* populations are presented in Table 4. Measures of genetic variability are given in Table 5. Modified Rogers' (Wright, 1978) and Nei's genetic distances (1972), calculated between all pairs of taxa are given in Table 6. Mean F_{ST} values and chi-square contingency table comparisons of all populations per species are summarized in Table 7. Data in Table 7 are grouped in analyses with and without Guadalupe Island populations, because these populations were significantly divergent.

Most populations of each species showed close genetic relationship (Tables 5–7). Heterozygosity and percent polymorphism levels for *H. rostratus* are somewhat higher than in species of *Gibbonsia.* All populations conformed to expected Hardy-Weinberg equilibria ($P > 0.70$). There was some deviation (not significant; $P > 0.44$) in the San Benito Islands sample of *G. elegans.* That deviation is the result of a single locus (sSod-A; Tables 4, 5). Contingency table, F_{ST} values, and genetic distances showed no significant temporal variation between samples analyzed by Waples (1986) and the present study. There was also no significant temporal variation between collections made in different years from sample sites at La Jolla (*G. elegans*) and the San Benito Islands (*H. rostratus* and *G. elegans*) (see Materials and Methods; Waples, 1986).

Allozymic differences among all populations of all species, except for those from Guadalupe Island, are minor (Tables 5–8; Figs. 2, 3). There are greater differences in populations from Guadalupe Island (Tables 5–8; Figs. 2, 3), which show closest relationship to San Benito Islands and other southern populations (Table 4; Fig. 2). Genetic variation between nominal subspecies and species (as defined by C. Hubbs, 1952) was tested with contingency chi-square tests (Table 8). No significant differences were found among intraspecific populations other than those from Guadalupe Island.

Relationships among taxa are summarized in Figures 2 and 3, which illustrate results of the distance Wagner procedure (Farris, 1972), based on modified Rogers' genetic distances (Wright, 1978). The tree shown in Figure 2, rooted with the South American myxodin *Myxodes viridis,* has a cophenetic correlation of 0.97. Cophenetic correlations for separate analyses of each individual species group are 0.97 for *H. rostratus,* 0.98 for *G. elegans,* 0.99 for *G. metzi,* and 0.99 for *G. montereyensis.*

All of the preserved specimens examined that fit the characters described by C. Hubbs (1952) for *G. erythra* (high dorsal fin and scales extending to the edge of the caudal peduncle) are males. Of 73 specimens examined that were originally identified as *G. erythra* in the SIO collection (and were large enough to be reliably sexed), 24 did not fit the characters. Of these, 19 were females (with caudal squamation patterns ranging from 1 to 3; see Fig. 4) and five were males (with caudal squamation patterns ranked 3). Eighty-six percent (85 of 99) of identifiable adult male *G. montereyensis* fit the characters of *G. erythra.* The remaining 14 specimens had intermediate patterns of squamation ranked 3 ($n = 10$) and 2 ($n = 4$; Table 9).

Specimens of *G. montereyensis* from several locations had scale patterns on the caudal peduncle ranging from the naked area on the pedun-

TABLE 4. GENOTYPIC DISTRIBUTIONS OF POLYMORPHIC LOCI FOR CLINID POPULATIONS.

Species and population	Polymorphic loci and number of each genotype												
	sAat-B	*sAcoh-A*	*Acp-A*	*Adh-A*	*Gpi-A*	*sIdh-A*	*Ldh-A*	*Ldh-B*	*Pep-A*	*Pgdh-A*			
H. rostratus													
1. Santa Catalina Island	aa:09 ab:01	aa:01 ab:05 bb:02	bb:08 ab:01	bb:05 ab:04	bb:07 ab:03	bb:07 ab:03	bb:06 ab:03	aa:07 ab:03	cc:09 ac:01	bb:07 ab:01			
2. San Diego	aa:29 ab:01 ac:01	aa:05 ab:15 bb:10	bb:15 ab:05 bc:01	aa:02 ab:12 bb:16	bb:26 ab:09	bb:20 ab:06	aa:02 ab:11 bb:17	aa:15 ab:09 bb:01	cc:26 ac:04	bb:25 ab:05			
3. Punta Clara	aa:06	ab:05 bb:01	bb:04 ab:02	ab:03 bb:03	bb:05 ab:01	bb:05 ab:01	bb:04 ab:02	bb:04 ab:02	cc:06	bb:05 ab:01			
4. San Benito Islands	aa:08 ab:01	aa:01 ab:04 bb:02	bb:09	ab:03 bb:07	bb:08 ab:01	bb:09 ab:01	bb:10	aa:08 ab:02	cc:08 ac:02	bb:09 ab:01			
5. Guadalupe Island*	aa:06	bb:05 ab:01	bb:05	bb:05	bb:05	bb:02	bb:04	aa:06	cc:05 ac:01	bb:05			
	sAat-B	*sAcoh-A*	*Acp-A*	*Adh-A*	*Est-3*	*Fumh-A*	*G3pdh-B*	*Gpi-A*	*Gpi-B*	*sMdh-B*	*Pep-A*	*Pgdh-A*	*Sod-A*
G. elegans													
1. San Simeon	aa:03	aa:03	aa:03	aa:02 ab:01	aa:03	aa:03	aa:02 ab:01	aa:02 ac:01	aa:03	aa:03	aa:03	aa:03	aa:02 ae:01
2. Santa Barbara	aa:09	aa:08	aa:08	aa:08	aa:07	aa:08	aa:07 ab:01	aa:08	aa:07 ac:01	aa:07 ab:01	aa:08	aa:07 ab:01	aa:06 ac:02 ae:01
3. Santa Cruz Island	aa:04	aa:04	aa:03 ad:01	aa:04	aa:04	aa:04	aa:04	aa:03 ac:01	aa:04	aa:04	aa:04	aa:04	aa:03 ac:01
4. Santa Catalina Island	aa:06 ab:01	aa:06 ab:01	aa:05 ad:02	aa:05	aa:05 ab:01 ac:01	aa:07	aa:05	aa:04 ac:01	aa:04	aa:06 ab:01	aa:07	aa:07	aa:06 ac:01
5. La Jolla	aa:56 ab:06	aa:53 ab:04 ac:06	aa:48 ad:05	aa:52 ab:03	aa:47 ab:03 ac:01	aa:47 ab:04	aa:50 ab:06 ac:03 ad:01	aa:45 ac:19 cc:02	aa:35 ac:02	aa:51 ab:10 ac:01	aa:63	aa:55 ab:04	aa:45 ac:06
6. Coronado Islands	aa:04 ab:01	aa:04 ac:01	aa:05	aa:05	aa:05	aa:05	aa:05	aa:04 ab:01	aa:05	aa:04 ab:01	aa:05	aa:05	aa:04 ac:01

TABLE 4. CONTINUED.

Species and population	Polymorphic loci and number of each genotype												
	sAat-B	*sAcoh-A*	*Acp-A*	*Adh-A*	*Est-3*	*Fumh-A*	*G3pdh-B*	*Gpi-A*	*Gpi-B*	*sMdh-B*	*Pep-A*	*Pgdh-A*	*Sod-A*
7. Punta Clara	aa:10	aa:06 ab:01 ac:01	aa:07	aa:08	aa:08 ab:01	aa:08	aa:07	aa:06 ac:02	aa:08 ac:01	aa:08 ab:01	aa:08	aa:07 ab:01	aa:07 ac:01
8. San Benito Island	aa:19 ab:01	aa:03 ac:01	aa:20	aa:10	aa:17 ab:01 ac:01	aa:17 ab:03	aa:19	aa:17 ac:02	aa:14 ac:01	aa:14	aa:16	aa:20	aa:15 ac:02 ec:01
9. Guadalupe Island**	aa:11 ab:01	ac:02 cc:01	aa:13	aa:09	aa:12	aa:13	aa:12 ab:01	aa:12 ad:01	aa:13	aa:13	aa:12 ab:01	aa:13	aa:10
	sAcoh-A	*Acp-A*	*Est-3*	*Fumh-A*	*Gpi-A*	*Gpi-B*	*sMdh-B*	*Pep-B*	*Pgdh-A*	*Pgm-A*	*Sod-A*		
G. metzi													
1. Carmel	aa:09 ab:02	aa:10 ad:01	aa:06	bb:09 ab:02	aa:07 ab:03 ac:01	aa:09	aa:08 ad:01 ab:01	cc:10 ac:01	bb:08 ab:02	bb:10 ab:01	aa:09 ac:01		
2. San Simeon	aa:41 ab:07 af:01	aa:41 ad:03	aa:38 ab:02 ac:01	bb:45 ab:07	aa:35 ab:12 ac:01	aa:44 ac:02	aa:46 ab:05 ad:02	cc:44 ac:04	bb:23 ab:05	bb:50 ab:02	aa:45 ac:02		
3. Punta Clara	aa:15 ab:03 af:03	aa:15 ad:02	aa:11 ab:03 ac:03	bb:16 ab:02	aa:15 ab:05	aa:15 ac:01	aa:07 ab:03	cc:15 bc:01	bb:17 ab:01	bb:15 ab:03	aa:16 ac:02		
	sAcoh-A	*Acp-A*	*Est-3*	*Fumh-A*	*G3pdh-B*	*Gpi-B*	*mIdh-A*	*sMdh-B*	*mMdh-A*	*Pep-3*	*Sod-A*		
G. montereyensis													
1. Carmel	aa:07 ab:02	aa:09 ad:01	aa:07 ab:01	bb:09	aa:09	aa:08 ac:02	bb:10	aa:10	bb:07 ab:02	dd:09 ad:01	aa:09 ac:01		
2. San Simeon	aa:21 ab:08 bb:01	aa:23 ad:02	aa:26 ab:02	bb:22 ab:03	aa:20 ab:01 ac:01	aa:22 ac:07	bb:29 ab:02	aa:28	bb:24 ab:06	dd:25 ad:03	aa:15 ac:04		
3. Santa Barbara	aa:03	aa:02 ad:01	aa:02 ab:01	bb:03	aa:03	aa:02 ac:01	bb:03	aa:03	bb:02 ab:01	dd:03	aa:03		
4. Punta Clara	aa:14 ab:04	aa:11 ad:05	aa:17 ab:01	bb:15 ab:02	aa:16	aa:14 ac:04	bb:17 ab:01	aa:15 ab:03	bb:17 ab:01	ad:01 dd:18	aa:16 ac:02		

TABLE 4. CONTINUED.

Species and population	Polymorphic loci and number of each genotype										
	sAcoh-A	*Acp-A*	*Est-3*	*Fumh-A*	*G3pdh-B*	*Gpi-B*	*mIdh-A*	*sMdh-B*	*mMdh-A*	*Pep-3*	*Sod-A*
*G. erythra***											
1. San Simeon	aa:06	aa:07	aa:07	bb:07	aa:07	aa:06	bb:08	aa:08	bb:06	dd:07	aa:07
	ab:02	ad:01				ac:02			ab:01	ad:01	ac:01
2. Coronado Islands	aa:03	aa:02	aa:04	bb:03	aa:04	aa:03	bb:04	aa:03	bb:04	dd:04	aa:04
	ab:01	ad:02		ab:01		ac:01		ab:01			
*G. norae****											
1. Guadalupe Island	aa:07	ad:03	aa:10	bb:07	aa:10	aa:02	bb:07	aa:09	bb:12	dd:12	aa:08
	ab:02	dd:07		ab:02	ac:01	ac:05		ab:02			ac:01
					ad:01	cc:03					

* = Allozyme data collected from 34 loci.
** = Allozyme data collected from 31 loci.
*** = Placed in the synonymy of *Gibbonsia montereyensis*.

cle characteristic of the species as described by C. Hubbs (1952) to squamation extending to the edge of the peduncle, characteristic of *G. erythra* (Fig. 4). In reexamining the scale patterns of 217 *G. montereyensis*, we found that significantly more males than females had a completely scaled caudal peduncle (Table 9). There were no significant differences between ratios of SH : HL ($\chi^2 = 2.11$, df = 1, $P = 0.15$) and SH : SL ($\chi^2 = 1.91$, df = 1, $P = 0.17$) for males (n = 102) versus females (n = 109). However, there were significant increases in these ratios with increasing depth (Table 10). There were no significant differences, however, between males from the 10 to 20 m and the 21 to 45 m classes. There was a significant difference between depth distributions of females and males (Table 11). Females dominated intertidal collections, decreasing in overall percentage with increasing depth, and males were most common subtidally, increasing in overall numbers with depth. Genetic distances based on allozyme data among samples identified from morphology as *G. erythra* and *G. montereyensis* are shown in Figure 3, further demonstrating that *G. erythra* cannot be separated genetically from *G. montereyensis*. Clustering reflects geographic, rather than morphotypic, relationships.

Reexamination of the characters distinguishing the Guadalupe Island endemic subspecies *G. elegans erroli* and *G. elegans rubrior* (purportedly differences in SH : HL and PL : HL ratios; C. Hubbs, 1952), from 103 specimens (38 females and 65 males) of known collection depths yielded similar results. Ratios of SH : HL and SH : SL were significantly greater in males than in females ($\chi^2 = 4.94$, df = 1, $P = 0.026$ and $\chi^2 = 5.92$, df = 1, $P = 0.015$, respectively). There was also a significant increase in SH : SL ratio with depth class for females ($\chi^2 = 6.71$, df = 2, $P = 0.035$) and a less significant increase in this ratio with depth for males ($\chi^2 = 2.96$, df = 1, $P = 0.85$). The holotype and three paratypes of *G. elegans rubrior* are all males and all have intermediate SH : HL and SH : SL ratios not significantly different from the mean of males in the population (Mean spine height: SL = 1.44, SD = 0.15, SE = 0.02 for males and SL = 1.35, SD = 0.22, SE = 0.04 for females). There were no significant differences between the sexes in PL : HL or PL : SL ratios ($\chi^2 = 0.40$, df = 1, $P = 0.84$ and $\chi^2 = 0.81$, df = 1, $P = 0.78$, respectively). Measures of PL : HL and PL : SL are directly correlated, and there is no evidence supporting C. Hubbs' (1952) supposition of bi-

TABLE 5. HETEROZYGOSITY AND POLYMORPHISM VALUES FOR POPULATIONS OF NORTHEASTERN PACIFIC CLINIDS.

Species	Population	Mean H per locus	Mean number of alleles per locus	% Polymorphism	
				Direct count	0.95 Criterion
H. rostratus	Catalina Island	0.07 + 0.02	1.25 + 0.07	25.00	25.00
	San Diego	0.07 + 0.02	1.30 + 0.09	25.00	22.50
	Punta Clara	0.07 + 0.03	1.20 + 0.06	20.00	20.00
	San Benito Islands	0.05 + 0.02	1.23 + 0.07	22.50	22.50
	Guadalupe Island*	0.01 + 0.01	1.04 + 0.04	03.57	03.57
G. elegans	San Simeon	0.03 + 0.02	1.10 + 0.05	10.00	10.00
	Santa Barbara	0.02 + 0.01	1.15 + 0.07	12.50	12.50
	Santa Cruz Island	0.02 + 0.01	1.08 + 0.04	07.50	07.50
	Catalina Island	0.03 + 0.01	1.20 + 0.07	17.50	17.50
	San Diego	0.04 + 0.01	1.42 + 0.12	30.00	12.50
	Coronado Islands	0.03 + 0.01	1.12 + 0.05	12.50	12.50
	Punta Clara	0.03 + 0.01	1.20 + 0.07	17.50	17.50
	San Benito Islands	0.02 + 0.01	1.23 + 0.08	17.50	12.50
	Guadalupe Island**	0.04 + 0.02	1.21 + 0.08	21.43	07.14
G. metzi	Carmel	0.04 + 0.01	1.27 + 0.09	22.50	15.00
	San Simeon	0.03 + 0.01	1.38 + 0.11	27.50	12.50
	Punta Clara	0.04 + 0.01	1.32 + 0.09	27.50	20.00
G. montereyensis	Carmel	0.03 + 0.01	1.17 + 0.06	17.50	17.50
	San Simeon	0.04 + 0.01	1.27 + 0.08	25.00	15.00
	Santa Barbara	0.03 + 0.02	1.10 + 0.05	10.00	10.00
	Punta Clara	0.03 + 0.01	1.23 + 0.07	22.50	15.00
*G. erythra****	San Simeon	0.03 + 0.01	1.15 + 0.06	15.00	15.00
	Coronado Islands	0.04 + 0.02	1.12 + 0.05	12.50	12.50
*G. norae****	Guadalupe Island	0.04 + 0.02	1.23 + 0.08	20.00	17.50

* = Allozyme data collected from 34 loci.
** = Allozyme data collected from 31 loci.
*** = Placed in the synonymy of *G. montereyensis*.

modality (the regression equation is PL = 0.1(SL) − 1.0; $R^2 = 0.94$, F = 1664, df = 1,101, $P < 0.0001$). Ratios of PL : HL and PL : SL of the holotype and paratypes of *G. elegans rubrior* are not significantly different from the mean of the population (Mean = 0.841, SD = 0.076, SE = 0.007). There was a significant difference between proportions of males versus females at various depths; only females were collected intertidally, and males were more common than females in subtidal waters (Table 11). All females collected subtidally were ripe, having gonadal maturities ranked 4 or 5.

DISCUSSION

Population relationships based on allozyme data.—Mean heterozygosity levels (direct count) for clinid populations (Table 5) approximate previous estimates from allozyme data for other marine fishes (Winans, 1980; Kirpichnikov, 1981; Beckwitt, 1983; Waples and Rosenblatt, 1987), including *G. metzi* (Somero and Soulé, 1974) and species of the labrisomid *Neoclinus* (Fukao and Okazaki, 1987). The Guadalupe Island sample of *Heterostichus* had significantly lower mean heterozygosity and polymorphism levels than the other populations. This may suggest a genetic bottleneck, either by an original colonization by a few individuals (founder effect) or a reduction in population in the relatively recent past (Holgate, 1966; Nei et al., 1975; Chakraborty and Nei, 1977). Alternatively, lower heterozygosity may be a result of selection. Giant kelp (*Macrocystis integrifolia*), which is one of the major habitats of *Heterostichus* (Stepien, 1986a, 1986b, 1987), is not present at Guadalupe Island (C. L. Hubbs, 1960), and the observed difference in genetic variability may be associated with habitat. It is possible that this low heterozygosity and polymorphism may be an artifact of small sample size. In contrast, Guadalupe Island populations of *G. elegans* and *G. montereyensis* have high hetero-

TABLE 6. NEI'S GENETIC DISTANCES (1972; BELOW DIAGONAL) AND MODIFIED ROGERS' GENETIC DISTANCES (WRIGHT, 1978; ABOVE DIAGONAL) BETWEEN ALL PAIRWISE COMBINATIONS OF POPULATIONS SAMPLED OF NORTHEASTERN PACIFIC MYXODIN CLINIDS.

Species	Population	Population 1	2	3	4	5	6	7	8	9
H. rostratus	1. Catalina Island	*****	0.025	0.022	0.045	0.109				
	2. San Diego	0.001	*****	0.022	0.057	0.117				
	3. Punta Clara	0.002	0.001	*****	0.049	0.108				
	4. San Benito Island	0.002	0.003	0.003	*****	0.089				
	5. Guadalupe Island*	0.012	0.014	0.012	0.008	*****				
G. elegans	1. San Simeon	*****	0.048	0.049	0.057	0.043	0.057	0.051	0.052	0.140
	2. Santa Barbara	0.002	*****	0.035	0.043	0.037	0.034	0.033	0.033	0.131
	3. Santa Cruz Island	0.002	0.001	*****	0.029	0.031	0.039	0.033	0.034	0.133
	4. Catalina Island	0.003	0.002	0.001	*****	0.030	0.035	0.033	0.037	0.126
	5. San Diego	0.002	0.001	0.001	0.001	*****	0.033	0.022	0.032	0.124
	6. Coronado Island	0.003	0.001	0.002	0.001	0.001	*****	0.031	0.034	0.123
	7. Punta Clara	0.003	0.001	0.001	0.001	0.000	0.001	*****	0.026	0.113
	8. San Benito Island	0.003	0.001	0.001	0.001	0.001	0.001	0.001	*****	0.106
	9. Guadalupe Island**	0.021	0.018	0.018	0.017	0.016	0.016	0.013	0.012	*****
G. metzi	1. Carmel	*****	0.007	0.013						
	2. San Simeon	0.000	*****	0.013						
	3. Punta Clara	0.001	0.001	*****						
G. montereyensis	1. Carmel	*****	0.018	0.029	0.036	0.012	0.048	0.149		
	2. San Simeon	0.000	*****	0.030	0.047	0.018	0.048	0.148		
	3. Santa Barbara	0.001	0.001	*****	0.043	0.030	0.053	0.133		
	4. Punta Clara	0.002	0.002	0.002	*****	0.041	0.023	0.131		
	5. San Simeon***	0.000	0.000	0.001	0.002	*****	0.045	0.146		
	6. Coronado Island***	0.002	0.002	0.003	0.001	0.002	*****	0.117		
	7. Guadalupe Island****	0.023	0.023	0.019	0.018	0.022	0.014	*****		

* = Allozyme data collected from 34 loci.
** = Allozyme data collected from 31 loci.
*** = *G. erythra*
**** = *G. norae*

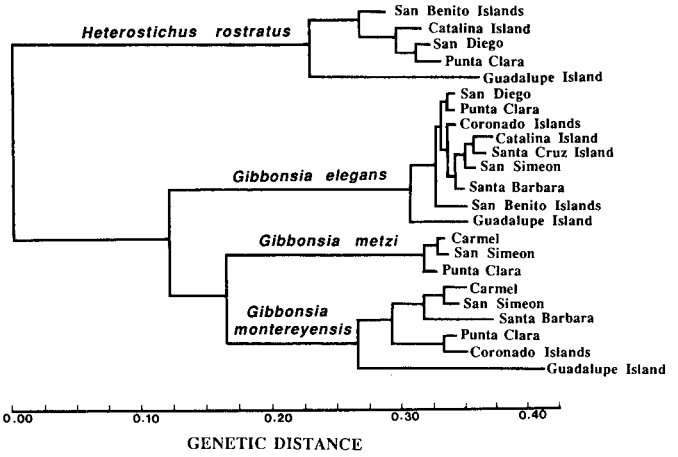

Fig. 2. Distance Wagner tree, illustrating relationships among clinid species and populations and showing relative genetic distances (add lengths of horizontal branches for genetic distances among taxa), rooted to the South American myxodin clinid *Myxodes viridis*.

zygosity and polymorphism levels in comparison to other populations and show some genetic divergence but no suggestion of recent bottlenecks.

Orton (1989), in the girellid *Girella nigricans*, found slightly greater genetic distances between Guadalupe Island and mainland populations than among mainland populations. This was largely a result of the presence of a unique allele at the sSod-A locus in the Guadalupe Island population.

Genetic distances (Table 6) and Wagner clustering relationships (Figs. 2, 3) show little genetic divergence among most clinid populations, excepting that from Guadalupe Island. Waples (1986, 1987) and Waples and Rosenblatt (1987) also found close genetic relationships between populations of several fishes from some of the same areas, including the Channel Islands, San Diego, Punta Eugenia–San Benito Islands, and Guadalupe Island; and Beckwitt (1983) found little variation between populations of three fish species in the southern California bight. However, Present (1987) found a significant allelic frequency difference between populations of the blenny *Hypsoblennius jenkinsi*

TABLE 7. SUMMARY OF F-STATISTICS AND CHI-SQUARE CONTINGENCY TESTS FOR ALLELIC VARIATION AMONG CLINID POPULATIONS, WITH AND WITHOUT GUADALUPE ISLAND SAMPLES.

Species and populations surveyed	Mean F_{ST}	Contingency comparisons		
		Chi-square	df	*P*
H. rostratus				
Without Guadalupe	0.02	29.83	39	>0.855
With Guadalupe	0.07	51.00	52	>0.513
G. elegans				
Without Guadalupe	0.05	116.39	140	>0.927
With Guadalupe	0.13	200.44	52	<0.005*
G. metzi	0.01	29.42	32	>0.598
G. montereyensis				
Without Guadalupe	0.04	39.02	60	>0.984
With Guadalupe	0.15	143.30	84	<0.001*

* = Significant deviation in frequencies of polymorphic alleles between populations based on chi-square contingency tests.

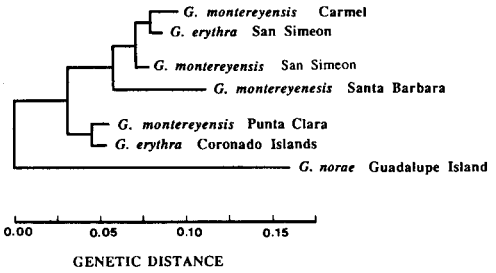

Fig. 3. Distance Wagner tree illustrating relationships among populations of *G. montereyensis, G. norae,* and *G. erythra* and showing relative genetic distances (add lengths of horizontal branches for genetic distances among taxa), rooted to *G. metzi.*

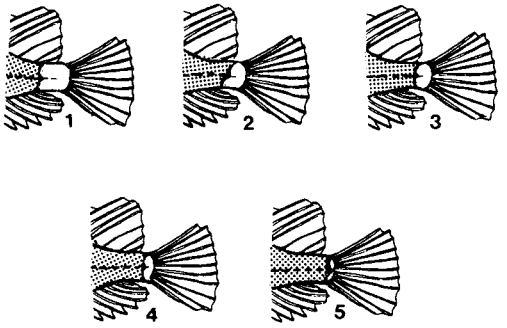

Fig. 4. Drawings of scale patterns on the caudal peduncle of *G. erythra* and *G. montereyensis.* Patterns are ranked from 1 to 5, according to extent of squamation (see Materials and Methods). Scales extend along the body to the point designated on the peduncle. Significant differences between male versus female scale patterns are shown in Table 9.

from two southern California locations, Scripps Pier (La Jolla) and San Diego Bay (separated by approximately 25 km), which was attributed to possible differences in local selection.

Swank (1979) found greater genetic distances separating populations of the cottid *Clinocottus analis* north and south of Point Conception (ranging from 0.006 to 0.044) than were found in the present study. The predominant allele at the Pgm-A locus in the central California populations was abruptly replaced by an alternate allele that predominated in the mainland populations of southern California and Baja California. Davis et al. (1981) found Nei's (1972) genetic distances separating populations of the hexagrammid *Oxylebius pictus* north versus south of Point Conception (ranging from 0.005 to 0.034) that were somewhat greater than those in the present study. This was largely because of the presence of two unique alleles at separate loci; one south and one north of Point Conception. Swank (1979) and Davis et al. (1982) found greater allelic divergences between localities north and south of Point Conception than were found for *G. elegans, G. montereyensis,* and *G. metzi* in the present study.

TABLE 8. CONTINGENCY COMPARISONS OF ALLELE FREQUENCIES AND NEI'S (1972) GENETIC DISTANCES AMONG SUBSPECIES AND CLOSELY RELATED SPECIES.

Taxon A and location	Taxon B and location	Genetic distance D	Chi-square		
			χ^2	df	*P*
H. rostratus guadalupensis Guadalupe Island	*H. rostratus rostratus* San Benito Islands	0.008	11.94	9	>0.217
G. elegans velifera La Jolla	*G. elegans elegans* La Jolla	0.000	16.09	10	>0.097
G. elegans erroli Guadalupe Island	*G. elegans elegans* San Benito Islands	0.012	7.44	17	>0.977
G. metzi ferventer Punta Clara	*G. metzi metzi* San Simeon	0.001	29.42	32	>0.597
G. montereyensis montereyensis Carmel	*G. montereyensis vulgaris* San Simeon	0.000	3.72	11	>0.978
G. erythra San Simeon	*G. montereyensis* San Simeon	0.000	3.28	11	>0.987
G. erythra Coronado Islands	*G. montereyensis* Punta Clara	0.001	2.13	9	>0.989
G. norae Guadalupe Island	*G. montereyensis* Punta Clara	0.018	43.21	12	<0.001

TABLE 9. CONTINGENCY TEST COMPARISONS OF SCALE PATTERN DISTRIBUTIONS (FIG. 3) AMONG MALE AND FEMALE *Gibbonsia montereyensis*.

Sex	Number	Scale pattern					Chi-square contingency test		
		1	2	3	4	5	χ^2	df	*P*
Males	99	00	04	10	36	49			
Females	118	08	57	42	11	00	135.41	4	<0.0005
	217	08	61	52	47	49			

Sassaman et al. (1983) found that Ldh-A in populations of the stichaeid *Anoplarchus purpurescens* ranging from Monterey Bay, California, through Alaska exhibited a longitudinal clinal trend, which was persistent throughout 10 years of sampling. They concluded that stability of geographical differences in allele frequency despite presumptive indications of extensive larval movement between sites suggested that selection, rather than isolation, was the prime force promoting this local differentiation. There is some evidence supporting longitudinal clinal allelic variation in the present study for *G. elegans*, *G. montereyensis*, and *G. metzi* (Table 6).

Heterostichus rostratus from Santa Catalina Island, San Diego, and Punta Clara have close genetic relationships; Santa Catalina and Punta Clara samples are slightly more genetically distant from each other than either is from the San Diego sample, reflecting geographic proximities. Close genetic relationships and little isolation of Channel Island populations from those of the mainland were also found by Waples (1986, 1987) and Waples and Rosenblatt (1987). However, Swank (1979) found the Catalina Island population of the cottid *Clinocottus analis* to be closer in genetic distance to populations north of Point Conception than to the southern California mainland. Orton (1989) found a significant difference in frequencies of one allele between populations of *Girella nigricans* from Santa Catalina Island and the mainland, although it is possible that this may be an artifact of sample size (n = 8 for the Santa Catalina Island population). Crabtree (1986) also found some genetic differences between populations of the atherinid *Atherinops affinis* from Santa

TABLE 10. CONTINGENCY TEST COMPARISONS OF FIRST DORSAL SPINE HEIGHT : SL AND SH : HL FOR *Gibbonsia montereyensis* FROM VARIOUS DEPTH CLASSES.

	Depth class			
	0–3 m	4–10 m	11–20 m	21–45 m
A. Spine height : head length				
Number sampled	87	78	16	30
Mean	0.53	0.54	0.62	0.57
Standard deviation	0.07	0.08	0.09	0.11
Standard error	0.01	0.01	0.02	0.02
Chi-square	10.43			
Degrees of freedom	3			
Probability	<0.001			
B. Spine height : standard length				
Number sampled	87	78	16	30
Mean	1.15	1.26	1.34	1.31
Standard deviation	0.12	0.19	0.17	0.22
Standard error	0.01	0.02	0.04	0.04
Chi-square	23.03			
Degrees of freedom	3			
Probability	<0.001			

TABLE 11. CONTINGENCY TEST COMPARISONS OF NUMBER OF MALE VERSUS FEMALE *Gibbonsia montereyensis* AND GUADALUPE ISLAND *Gibbonsia elegans* COLLECTED AT VARIOUS DEPTHS.

	Depth class			
	0–3 m	4–10 m	11–20 m	21–45 m
A. *Gibbonsia montereyensis*				
Number of females	75	22	06	06
Number of males	12	56	10	24
Totals	87	78	16	30
Chi-square	72.09			
Degrees of freedom	3			
Probability	<0.0001			
B. *Gibbonsia elegans* (Guadalupe Island population)				
Number of females	07	25	06	—
Number of males	00	42	23	—
Totals	07	67	28	—
Chi-square	15.25			
Degrees of freedom	2			
Probability	<0.001			

Catalina Island and the mainland. The Santa Catalina Island population was most similar to the population sampled from Cedros Island, Baja California, Mexico (which is near San Benito Islands), largely because of lack of a single gene product at a single locus.

The San Benito Islands population of *Heterostichus* is closest in genetic distance to that of Santa Catalina Island, which appears to be similar to Crabtree's (1986) findings for *Atherinops affinis*. Waples and Rosenblatt (1987) also found that San Benito Islands–Punta Eugenia fish populations are more genetically different than those from northern sites and that in most species the closest relationship was to Santa Catalina Island samples, the remainder to La Jolla (San Diego) samples.

Heterostichus from Guadalupe Island are genetically separable from other populations, and their closest relationship is to the San Benito Islands population. For example, both the Guadalupe and San Benito populations uniquely share the losses of the "a" allele at the Acp-A locus and the "a" allele at the Ldh-B locus. These results are similar to relationships between San Benito and Guadalupe Island populations for the labrisomid *Alloclinus holderi* determined by Waples and Rosenblatt (1987).

Individuals of *G. elegans* from San Simeon were collected north of their primary range in Oct. 1986, and were determined (using otolith rings) to be three years old. It is possible that they were recruited from larvae transported north during the 1982 to 1983 El Niño. Our sampling, as well as that by others from this area (in the SIO collection records), indicate that *G. elegans* is relatively rare north of Point Conception.

Our data also are consistent with high levels of gene flow among all populations of *G. elegans* sampled, with genetic relationships largely reflecting geographic proximity (Table 6; Figs. 2, 3). The data also suggest some north to south clinal variation. For example, the "c" allele for the sAcoh-A locus is absent from the four northerly population samples and increases in frequency southward from its appearance in the La Jolla sample. The "b" allele for Est-3 follows a similar pattern, increasing in frequency southward from its appearance in the Santa Catalina Island sample. There are also two cases of apparent allelic absence at geographic extremes. The "b" allele of sMdh-B is absent from the two northernmost populations (San Simeon and Santa Cruz Island) and the two southernmost populations (San Benito and Guadalupe Islands) sampled, and the "b" allele at the sAcoh-A locus is absent from the three northernmost populations (San Simeon, Santa Cruz Island, and Santa Barbara), as well as from the San Benito and Guadalupe islands populations. The "d" allele at the Acp-A locus is present only in the

northernmost populations sampled south of Point Conception (Santa Cruz Island, Santa Catalina Island, and La Jolla; Table 4).

Genetic distance data suggest that the San Benito Islands population is little divergent from the other samples, excepting Guadalupe Island. However, the San Benito population is closer in genetic distance to that of Guadalupe Island than are the other populations, as is the case in *Heterostichus*. Guadalupe Island populations of *G. elegans* and *Heterostichus* are greater in genetic distance from other sites but show closer relationship to southern than northern populations.

Populations of *G. metzi* north of Point Conception and in the coldwater upwelling site at Punta Clara (off Baja California) are close in genetic distance (Table 6; Fig. 2). This species has a somewhat disjunct distribution pattern because it is rare off coastal southern California and the offshore islands, reappearing in large numbers in these cold water upwelling areas off Baja California (C. Hubbs, 1952; Stepien et al., 1991). C. Hubbs (1952) considered the populations of *G. metzi* north and south of Point Conception to be subspecifically different. Genetic distances in the present study suggest that this separation is unjustified because even the widely separated areas sampled in the present study show little appreciable genetic divergence. There is some allelic variation between the disjunct populations: notably absence of three alleles in the Punta Clara sample that are present north of Point Conception; the "c" allele at the Gpi-A locus; the "d" allele at the sMdh-B locus; and the "a" allele at the Pep-B locus. The Punta Clara population also has a "b" allele at the Pep-B locus that is absent from samples north of Point Conception. However, this variation in rare alleles, which may reflect clinal differences, and the close genetic distance between them, indicates that they should not be subspecifically separated.

Samples of *G. montereyensis* north of Point Conception and in the Punta Clara upwelling site show also close genetic relationship, consistent with apparent high levels of gene flow (Table 6; Figs. 2, 3). Samples fitting the characters of the nominal *G. erythra* described by C. Hubbs (1952) cannot be separated genetically from *G. montereyensis* (Fig. 3), indicating that *G. erythra* should be placed in the synonymy of *G. montereyensis*. These results are further supported by morphological data, as discussed in the next section. Guadalupe Island samples of the nominal species *G. norae*, erected by C. Hubbs (1952) as endemic to Guadalupe Island and San Benito Islands, show genetic separation comparable to that found in *G. elegans* and *H. rostratus*. These results, together with the paucity of morphological characters delimiting *G. norae* (see next section on morphological variation), suggest that it should be at most a subspecies of *G. montereyensis*.

Genetic distances separating the Guadalupe Island populations of all three clinid species are comparable to those separating other semiisolated fish populations (Vawter et al., 1980; Waples, 1986, 1987; Waples and Rosenblatt, 1987; Grant and Stahl, 1988). These genetic distances (as well as data on morphological variation; see next section) are considerably less than those separating congeneric clinid (Stepien, 1992; see Fig. 2) and labrisomid species (Fukao and Okazaki, 1987; Stepien, 1992). Additionally, Thorpe (1983), utilizing 900 congeneric species comparisons, noted that only some 2% have Nei's (1972) D values below 0.16 and only 0.5% below 0.1.

There is additional support for north-south clinal trends in allelic frequencies in populations of *G. montereyensis* (including *G. erythra* and *G. montereyensis*). The frequency of the "d" allele at the Acp-B locus increases significantly from north to south, with greatest frequency at Guadalupe Island. There are similar southward increases in the frequencies of the "b" allele at the Fum-A locus and the "c" allele at the G3pdh-B locus. There is a unique "d" allele present at the G3pdh-B locus in the Guadalupe Island population.

As in the other clinids, the Guadalupe Island population of *G. montereyensis norae* shows closer genetic relationship to southern populations than to those north of Point Conception. Unfortunately, samples of *G. m. norae* from the San Benito Islands were not obtained in the present study. Waples (1986, 1987) and Waples and Rosenblatt (1987) found that six out of eight species of Guadalupe Island fishes (other than clinids) were closer in genetic relationship to populations from the Channel Islands and La Jolla than to those of the San Benito Islands. Populations of several fishes from San Benito Islands and Punta Eugenia, Baja California (pooled by Waples and Rosenblatt), showed almost as much genetic isolation from northern populations as did those from Guadalupe Island. Relationships of clinid populations from these areas are consistent with those determined by Waples (1987) and Waples and Ro-

senblatt (1987) for the labrisomid *Alloclinus holderi* and the labrid *Semicossyphus pulcher*.

Mean F_{ST} values for each species (Table 7) indicate little overall genetic variation among populations of *H. rostratus* and *G. metzi* and moderate variation among those of *G. elegans* and *G. montereyensis*, when Guadalupe Island populations are not included (according to genetic divergence levels specified by Wright, 1978, and Hartl and Clark, 1989). With inclusion of Guadalupe Island, *Heterostichus* and *G. elegans* exhibit moderate levels of variation and *G. montereyensis* (including *G. montereyensis norae*) borders on moderate to great genetic variation. Chi-square tests (Tables 7, 8) show no significant differences in overall frequencies of polymorphic alleles among populations of all species and subspecies, when Guadalupe Island populations are excluded. However, there are significant differences in overall allelic frequencies among populations of *G. elegans* and *G. montereyensis* when Guadalupe Island populations are included. The following loci vary significantly: sAcoh-A and Gpi-A in *G. elegans* and Acp-2 and Gpi-B in *G. montereyensis*.

Morphological variation.—C. Hubbs' (1952) analysis of the northeastern Pacific myxodin clinids was based on meristic data, body proportions, and combinations of meristic counts, many of which overlap considerably among groups and show depth-related variation. In examining preserved clinids and samples collected for allozyme data, we found almost all clinid samples to be biased in sex ratio, being either mostly adult males (samples from subtidal waters) or females and juveniles (intertidal samples; see Table 11). This pattern of depth segregation by sex has been previously described for *G. elegans* (Williams, 1954; Stepien et al., 1988; data from the Guadalupe Island population examined in the present study are summarized in Table 11) and *H. rostratus* (Stepien, 1986a, 1987). The same pattern occurs in *G. metzi* and *G. montereyensis* (Table 11), according to material examined in the present study, as well as in the South American myxodin clinid *Myxodes viridis* (Stepien, 1990). Mature female myxodin clinids (e.g., *H. rostratus*) briefly migrate to male territories in deeper water during the spring spawning season to lay eggs in algal nests, which the males guard until hatching (Stepien, 1986a, 1987). If morphological variation between populations and taxa is to be analyzed, depth segregation of the sexes necessitates sexing of all clinid material, as was done in the present study.

Northeastern Pacific myxodin clinids are sexually dimorphic in size; adult females are larger than males at given ages and attain greater lengths (Stepien, 1968a, 1987; Stepien et al., 1988). Such size dimorphism was previously suggested by C. Hubbs (1952) for *G. metzi* and occurs in all species examined in the present study.

In addition, there is sexual dichromatism in *Heterostichus rostratus* (color morphs; Stepien, 1986b, 1987) and *G. elegans* (belly color; Stepien et al., 1988). Deepwater male *G. elegans* (designated as *G. elegans velifera* and *G. elegans rubrior* by C. Hubbs, 1952) and *G. montereyensis* (designated as *G. erythra*) have distinctive red or red-brown color patterns with prominent ocelli on the body above the lateral line (C. Hubbs, 1952; Stepien, unpubl.). Their color matches the red algae among which they live and guard nests. Females and juveniles in shallower areas occur in a variety of red, green, and brown color patterns, which also match their algal habitats (Stepien et al., 1988). Some of these variations in color pattern were considered by C. Hubbs (1952) to characterize various subspecies. Results of the present study suggest that color pattern variation within taxa (red and red-brown colors of deepwater specimens of *G. elegans erythra*, *G. elegans rubrior*, and *G. erythra*) is correlated with depth and algal habitat and, in some cases, sex.

C. Hubbs (1952) divided *G. metzi* into two subspecies, *G. m. metzi* north, and *G. m. ferventer* south, of Point Conception on the basis of slight differences in lengths of the caudal peduncle and first anal soft ray, stating, "When these two measurements are added and their proportion to the standard length plotted, their standard deviations scarcely overlap." Allozyme data are consistent with the hypothesis of extensive gene flow between these widely separated populations (central California versus Baja California, Mexico; see Fig. 2) and do not substantiate subspecies designation.

Shallow and deepwater populations of *G. elegans* were separated as the subspecies *G. elegans elegans* and *G. elegans velifera*, which differed slightly in relative proportions of SH : HL and body depth : SL, but not in any meristic characters (C. Hubbs, 1952). Williams (1954) examined 777 specimens of *G. elegans* from various depths and found significant differences in sex ratio between shallow and deepwater collections (primarily females in the former and a greater number of males in the latter). Williams' data showed that morphological differences dis-

tinguishing *G. elegans elegans* and *G. elegans velifera* were gradual changes resulting from depth-related phenotypic variation. He concluded that differences in sex ratio and morphological intergradiation between the two forms indicated that they represent a single population. In the present study, contingency chi-square tests showed no significant allelic variation between deep water *G. elegans velifera* (all males) and shallow *G. elegans elegans* (both males and females; La Jolla sample sites; see Table 8), further corroborating Williams' conclusions.

C. Hubbs (1952) also described two Guadalupe Island subspecies, *G. elegans erroli* and *G. elegans rubrior,* as differing from each other in the same body proportions purportedly distinguishing *G. elegans velifera* from *G. elegans elegans. Gibbonsia elegans rubrior* was described from four specimens (the holotype and paratypes; which were examined in the present study and found to be males); we were not able to obtain any for allozyme work. Allozyme data were analyzed from six intertidal specimens identified as *G. elegans erroli.* Examination of morphological characters from preserved material demonstrated that proportional differences supposedly distinguishing *G. elegans erroli* from *G. elegans rubrior* are also a result of sexual dimorphism and depth-related variation.

C. Hubbs (1952) found that the Guadalupe Island population of *G. elegans* differed from those of the mainland by having fewer dorsal spines (31 to 33 versus 32 to 35), as well as in some body proportions. The Guadalupe population was regarded as most similar in morphology to that of the San Benito Islands, which have similar temperatures (Table 1). These population relationships are mirrored by results of the present study based on allozyme data (Table 6; Fig. 2). Allozyme data, sex differences in depth distribution, and morphological evidence suggest that subspecies of *G. elegans* need not be recognized.

Guadalupe Island samples of all three species (*Heterostichus, G. elegans,* and *G. montereyensis*) have somewhat reduced meristic counts, notably number of fin rays, and this is probably related to warmer temperatures (Lynn et al., 1982; Table 1). Many other fishes exhibit temperature-related variation in meristics, such as fin ray counts, which are reduced in warmer waters (C. L. Hubbs, 1926; Barlow, 1961). The lower counts are correlated with more rapid development at these temperatures and are, thus, not usually genetic. In all cases except one, the Guadalupe Island meristic counts broadly overlap with those of other populations and are closest to the San Benito Islands and central Baja California populations (C. Hubbs, 1952). A possible exception is the reduced number of scale rows above the lateral line in *G. norae* (samples pooled from San Benito and Guadalupe islands), which does not overlap those of *G. montereyensis* examined by C. Hubbs (1952). However, this lack of overlap may be an artifact of sampling, because C. Hubbs (1952) did not include any samples from the mainland south of Ensenada.

C. Hubbs named two subspecies of *G. montereyensis* from areas of high wave action (*G. m. montereyensis*) and lesser wave action (*G. m. vulgaris*), the latter being more common and widely distributed. These subspecies were distinguished on the basis of overlapping differences in relative height of SH and eye diameter. They were not separated by any meristic characters. Specimens from the Soberanes Point, Carmel site were identified as *G. m. montereyensis,* purportedly found only on the Monterey Peninsula and at Port Buchon (C. Hubbs, 1952). All other populations corresponded to *G. m. vulgaris.* Our examinations of preserved material show that SH is correlated with depth (Table 10), as in *G. elegans* (Williams, 1954). Allozyme data show no genetic differences between these subspecies (Tables 4, 6, 8; Figs. 2, 3), and the proportional differences appear nominal and a result of ecological variation.

Gibbonsia norae, endemic to San Benito and Guadalupe islands, was separated from *G. montereyensis* by C. Hubbs (1952) on the basis of a smaller number of scale rows above the lateral line and fewer dorsal and anal-fin rays. The former character is the only one distinguishing *G. norae,* because the others show extensive overlap. Lower meristic counts in the San Benito and Guadalupe islands populations are common to all three clinid species and may be a result of their more rapid development in warmer water (Barlow, 1961). Lack of morphological characters distinguishing *G. norae* from *G. montereyensis,* absence of fixed allelic differences, and the relatively small genetic distance separating them (which is comparable to those seen in other Guadalupe Island clinids) indicates that species-level separation is unwarranted. We, thus, suggest that *G. norae* be placed in the synonymy of *G. montereyensis.*

Gibbonsia erythra was said to be found primarily in deeper habitats along southern California, the Channel Islands, and northern Baja California, Mexico (C. Hubbs, 1952). The species was separated from *G. montereyensis* on the

basis of scales extending to the edge of the caudal peduncle (as opposed to a naked area on the peduncle characteristic of *G. montereyensis*) and a higher SH. In all but one of the records from the SIO and Los Angeles County Museum (LACM) collections in which more than one specimen was collected (n = 6), *G. erythra* were collected sympatrically with *G. montereyensis*. We found that all *G. erythra* (fitting the characters given by C. Hubbs, 1952) are males. Additionally, 86% of male *G. montereyensis* fit the definition of *G. erythra*. We examined caudal peduncle squamation in 217 adult *G. montereyensis* from these collections and the fresh material used in the present study. The amount of squamation on the caudal peduncle in *G. montereyensis* varies extensively, ranging from C. Hubbs' (1952) drawing of the pattern characteristic of *G. erythra* to that of *G. montereyensis*. However, patterns of few individuals fit either of these extremes. Scales usually extend further along the sides of the peduncle and in the center (Fig. 4). Our results show that extent of the naked area on the peduncle is correlated with sex (Table 9), females having a significantly lesser degree of squamation than do males. This difference was apparent in the smallest specimens. Allozyme data in the present study demonstrate that there is no genetic divergence between *G. erythra* and *G. montereyensis* (Tables 4, 6; Fig. 3).

Height of the anterior portion of the dorsal fin in the nominal *G. erythra*, as in the nominal *G. elegans velifera* (Williams, 1954), *G. elegans rubrior*, and *G. montereyensis vulgaris*, is positively correlated with depth and characteristic of deep water male-dominated samples. Results of the present study suggest that *G. erythra* and *G. norae* should be placed in the synonymy of *G. montereyensis* (see Table 2). The following key distinguishes the northeastern Pacific clinid species:

Key to the Northeastern Pacific Clinidae

1A. Caudal fin forked; snout sharply pointed; more than 30 anal soft rays; 11 or more dorsal soft rays ..... *H. rostratus*

1B. Caudal fin slightly rounded; snout not sharply pointed; fewer than 30 anal soft rays; 10 or fewer dorsal soft rays 2

2A. Dorsal soft rays relatively evenly spaced; 7 to 10 dorsal soft rays; ocelli on the body above the lateral line either small or absent ..... *G. metzi*

2B. Posterior dorsal soft rays markedly more widely spaced than anterior rays; 4 to 8 dorsal soft rays; often 2 or more ocelli on the body above the lateral line 3

3A. Scales extending well onto caudal rays in both sexes ..... *G. elegans*

3B. No (or very few) scales on caudal fin; females often with a scaleless gap on the caudal peduncle ..... *G. montereyensis*

Patterns of gene flow and distribution.—Patterns of genetic relationships among populations of all four clinid species may reflect similarities in their life histories, length of larval phase, dispersal patterns, and/or selective forces. Stepien (1986a) found larvae of *Heterostichus* to be planktonic for approximately two months, and species of *Gibbonsia* appear to share that length of larval life (Stepien, unpubl.). Larval collection data show that clinids are sometimes collected some distance offshore throughout the southern California bight (G. Moser and G. McGowen, pers. comm.; Stepien, unpubl.), and the species may, thus, be capable of long distance dispersal. In addition, adults and juveniles have been found rafting offshore in pieces of drift algae (Stepien, unpubl.). This capacity for dispersal may account for the apparent high levels of genetic uniformity found among clinid populations.

In the present study, disjunct populations of the cooler-water species, *G. metzi* and *G. montereyensis* showed surprisingly little genetic divergence considering the distance between the sites north of Point Conception and at the Punta Clara, Baja California upwelling site. South of Point Conception, these species are found in cold water locations such as the upwelling areas of northern Baja California, as well as subtidally off the mainland and some of the Channel Islands (C. Hubbs, 1952; Stepien et al., 1991). The combination of long planktonic larval life and coastal current patterns (Fig. 1) may also serve to transport them long distances before settlement, maintaining high levels of gene flow.

Patterns of genetic relationships among populations of all species corresponded to geographic proximities. Presumed gene flow patterns also appear related to the major offshore currents (Fig. 1), which probably serve as avenues of larval transport. For example, the Channel Islands are little divergent from mainland populations, as found in other studies of fishes by Waples (1986, 1987) and Waples and Rosenblatt (1987). Similarly, populations of *G. elegans* and *G. montereyensis* from the Coronado Islands off northern Baja California are genet-

ically close to Punta Clara and San Diego populations. Among populations of *G. elegans*, one of the closest genetic relationships is between Santa Catalina and Santa Cruz islands, which are linked by the offshore eddy pattern shown in Figure 1. In contrast to our findings, Haldorson (1980) found significant variation in gene frequencies between Santa Cruz Island and mainland populations of two species of surfperches (Embiotocidae), which may be linked to their viviparity and consequent reduced vagility. Our results suggest that populations from the San Benito Islands are only slightly divergent from mainland populations, which corresponds to their proximity to the nearest mainland and their apparent link with currents passing close to the mainland (Fig. 1).

The three clinid populations from Guadalupe Island (*Heterostichus, G. elegans* and *G. montereyensis norae*) are significantly more genetically isolated from the other populations. Genetic distances distinguishing them are similar but slightly greater in *G. montereyensis*, which may be a result of its being primarily a more northern (cold water) species. Relative genetic isolation of Guadalupe is probably a result of a combination of factors, including its small size and sharp drop-off (limiting shallow water algal areas available for clinid habitats), considerable distance from mainland and other island populations, the surrounding realm of very deep water, and current patterns that only remotely link it with other clinid populations (Fig. 1). These factors may account for genetic drift and/or natural selection resulting in the divergence of these populations. These populations show a very small degree of genetic divergence and, therefore, no clear-cut genetic characteristics to support their recognition as separate species. Although temperature tolerance experiments (Davis, 1977) showed that *G. metzi* has greater tolerance for warm temperatures than does *G. montereyensis, G. metzi* has not been collected at either the San Benito or Guadalupe islands.

Summary.—In conclusion, although the four species of North American clinids, as defined in the present study, display two general patterns of distribution, either primarily in cooler waters (north of Point Conception and in areas of cold water upwelling) or in warmer waters (south of Point Conception), there is considerable sympatry in the southern coastal upwelling areas, as well as off some of the offshore islands. Our results are consistent with high gene flow among all areas sampled (except Guadalupe Island), including the disjunct populations of the former group, which appears to reflect their high capacity for dispersal. The geographic isolation of Guadalupe Island accounts for the genetic divergence of its clinid populations. There is also some evidence supporting north-south clinal geographic variation, which may suggest temperature-related selection.

Material Examined

Specimens used for allozyme analyses and voucher specimen numbers.—*Heterostichus rostratus* 10 between 5 and 15 m in depth, Santa Catalina Island, California (SIO 90-81); 35 from trawl samples 5 to 10 m deep, Mission Bay, San Diego (SIO 90-80); 6 intertidally, Punta Clara, Baja California, Mexico (SIO 90-82); 10 between 0 and 15 m in depth, San Benito Islands, Baja California, Mexico (SIO 90-83); 6 between 0 and 20 m in depth, Guadalupe Island, Baja California, Mexico (SIO 90-84); *G. elegans elegans* 3 intertidally, San Simeon, California (SIO 90-88); 9 between 0 and 5 m in depth, Santa Barbara, California (SIO 90-87); 4 between 5 and 15 m in depth, Pelican Bay, Santa Cruz Island, California (SIO 90-90); 10 between 5 and 10 m in depth from Cherry Cove, Santa Catalina Island, California (SIO 90-81); 53 intertidally from Bird Rock, La Jolla, California (SIO 90-85); 5 between 5 and 30 m in depth, Middle Coronado Island, northern Baja California, Mexico (SIO 90-89); 10 intertidally, Punta Clara, Baja California, Mexico (SIO 90-82); 20 between 0 and 20 m in depth, San Benito Islands, Baja California, Mexico (SIO 90-83); *G. elegans velifera* 11 from 10 and 15 m depth, Boomer Beach, La Jolla, Calfornia (SIO 90-86); *G. elegans erroli* 13 intertidally, Guadalupe Island, Baja California, Mexico (SIO 90-84); *G. metzi metzi* 11 intertidally, Soberanes Point, Carmel, California (SIO 90-91); 53 intertidally, San Simeon, California (SIO 90-88); *G. metzi ferventer* 21 intertidally, Punta Clara, Baja California, Mexico (SIO 90-82); *G. montereyensis vulgaris* 10 intertidally Soberanes Point, Carmel, California (SIO 90-91); *G. montereyensis montereyensis* 31 intertidally, San Simeon, California (SIO 90-88); 3 between 10–20 m in depth, Santa Barbara, California (SIO 90-87); 19 intertidally, Punta Clara, Baja California, Mexico (SIO 90-82); *G. norae* 12 intertidally, Guadalupe Island, Mexico (SIO 90-84); *G. erythra* 8 in deep tidepools, San Simeon, California (SIO 90-88); 4 between 20 and 35 meters in depth, middle Coronado Island, Baja California, Mexico (SIO 90-89); *Myxodes viridis* (South American myxodin clinid used for tree rooting) 30 intertidally from Montemar, Vina del Mar, Chile (SIO 87-132).

Preserved material examined.—*G. montereyensis* SIO 73-220, Piedras Blancas Point, San Luis Obispo, California (20); SIO 80-21, Piedras Blancas Point, San Luis Obispo (19); SIO 69-245-61, San Simeon, San Luis Obispo (10); LACM 39975-9, San Simeon (10); SIO 67-151, San Simeon (60); SIO H47-97, Santa Rosa Island (1); SIO H51-244, Santa Cruz Island (2); SIO H51-227, Santa Catalina Island (5); SIO H48-122, Point Loma (1), SIO H51-23, Punta Banda, Baja California, Mexico (23); SIO H49-173, Rio Santo Tomas (5); SIO 61H47-203, Punta Clara (54); SIO 52-158-61A, San Geronimo Island (17); *G. erythra* SIO 51-244, Santa Cruz Island, California (8); SIO 51-240-61A, Santa Cruz Island (1), SIO 51-249, Santa Cruz Island (32); SIO 51-260-61, SIO 51-251, Santa Cruz island (20); LACM 3-9975-9, San Simeon (7); Santa Rosa Island (1); SIO 51-241-61A, Santa Rosa Island (1); SIO 51-241-61B, Santa Rosa Island (1); SIO 54-190-61, San Miguel Island (1); SIO 58-502-61A, La Jolla (1); SIO 61-527-61A, La Jolla (1); SIO H49-151, South Coronado Island, Baja California, Mexico (2); SIO 58-481-61, Coronado Islands (6); SIO 59-305-61C, Punta Banda (1); SIO H52-215, Bahia San Carlos (1); *G. norae* SIO 65-71, Guadalupe Island, Mexico (8); SIO 65-51, Guadalupe Island (1); SIO 57-190, Guadalupe Island (3); SIO 63-178, Guadalupe Island (2); SIO 70-49, Guadalupe Island (5); SIO 58-492, Guadalupe Island (1); SIO 60-15, Guadalupe Island (3); SIO 63-174, Guadalupe Island (2); SIO 71-108, Guadalupe Island (2); SIO H51-124-61A, Guadalupe Island (7); *G. elegans rubrior* CAS SU 16272, holotype, Guadalupe Island (1); CAS SU 16272, paratypes, Guadalupe Island (3); *G. elegans erroli* and *G. elegans rubrior* (mixed) SIO

50-38, Guadalupe Island (25); SIO 54-213, Guadalupe Island (6); SIO 58-453, Guadalupe Island (18); SIO 58-492, Guadalupe Island (20); SIO 58-497, Guadalupe Island (8); SIO 60-14, Guadalupe Island (15); SIO 60-14-16C, Guadalupe Island (2); SIO 63-184-61B, Guadalupe Island (5).

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Literature Cited

Abbott, I. A., and G. J. Hollenberg. 1976. Marine algae of California. Stanford Univ. Press, Stanford, California.

Barlow, G. W. 1961. Causes and significance of morphological variation in fishes. Syst. Zool. 10: 105–117.

Beckwitt, R. 1983. Genetic structure of *Genyonemus lineatus, Seriphus politus* (Sciaenidae) and *Paralabrax clathratus* (Serranidae) in Southern California. Copeia 1983:691–696.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill, New York, New York.

Buth, D. G., and R. W. Murphy. 1990. Appendix 1: Enzyme staining formulas, p. 99–126. *In:* Molecular systematics. D. M. Hillis and C. Moritz (eds.). Sinauer Associates, Sunderland, Massachusetts.

Chakraborty, R., and M. Nei. 1977. Bottleneck effects on average heterozygosity and genetic distance with the stepwise mutation model. Evolution 31:347–356.

Cooper, J. G. 1864. On new genera and species of California fishes. Proc. California Acad. Sci., ser. 1. 3:108–114.

Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. J. Mar. Res. 43:719–742.

Crabtree, C. B. 1986. Systematics and taxonomy of the members of the Atherinopsinae (Pisces: Atherinidae). Unpubl. Ph.D. diss., Univ. of California, Los Angeles.

Davis, B. J. 1977. Distribution and temperature adaptation in the teleost fish genus *Gibbonsia*. Marine Biol. 42:315–320.

———, E. E. de Martini, and K. McGee. 1981. Gene flow among populations of a teleost (painted greenling, *Oxylebius pictus*) from Puget Sound to southern California. *Ibid.* 65:17–23.

Dawson, E. Y. 1960. A review of the ecology, distribution, and affinities of the benthic flora. Symposium: the biogeography of Baja California and adjacent seas. Syst. Zool. 9:93–100.

Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. Am. Nat. 106:645–668.

Fukao, R., and T. Okazaki. 1987. A study on the divergence of Japanese fishes of the genus *Neoclinus*. Japan J. Ichth. 34:309–323.

Garth, J. S. 1960. Distribution and affinities of brachyuran Crustacea. Symposium: the biogeography of Baja California and adjacent seas. Syst. Zool. 9:105–123.

Girard, C. F. 1854. Observations on a collection of fishes made on the Pacific coast of the United States by Lieut. W. P. Trowbridge, U.S.A., for the Museum of the Smithsonian Institution. Proc. Acad. Nat. Sci. Philadelphia 7:142–156.

Grant, W. S., and G. Stahl. 1988. Evolution of Atlantic and Pacific cod: loss of genetic variation and gene expression in Pacific cod. Evolution 42: 138–146.

Greenfield, D. W., and J. W. Wiley. 1968. Geographic variation in the clingfish *Gobiesox eugrammus* Briggs. Trans. San Diego Soc. Nat. Hist. 15: 131–147.

Haldorson, L. 1980. Genetic isolation of Channel Islands fish populations: evidence from two embiotocid species, p. 433–442. *In:* the Channel Islands: proceedings of a multidisciplinary symposium. D. M. Powers (ed.). Santa Barbara Museum Natural History, Santa Barbara, California.

Hartl, D. L., and A. G. Clark. 1989. Principles of population genetics. 2d ed. Sinauer Assoc., Inc., Sunderland, Massachusetts.

Hedgepeth, J. W. 1957. Marine biogeography, p. 459–482. *In:* Treatise on marine ecology and paleoecology. I. Ecology. J. W. Hedgpeth (ed.). Geol. Soc. Amer. Mem. 67. New York, New York.

Hickey, B. M. 1979. The California current system—hypotheses and facts. Prog. Oceanogr. 8:191–279.

Holgate, P. 1966. A mathematical study of the founder principle of evolutionary genetics. J. Appl. Prob. 3:115–128.

Horn, M. H., and L. G. Allen. 1978. A distributional analysis of California coastal marine fishes. J. Biogeogr. 5:23–42.

Hubbs, C. 1952. A contribution to the classification of the Blennioid fishes of the family Clinidae, with a partial revision of the eastern Pacific forms. Stanford Ichth. Bull. 4:41–165.

HUBBS, C. L. 1926. The structural consequences of modifications of the development rate in fishes, considered in reference to certain problems of evolution. Am. Nat. 60:57–81.

———. 1927. Notes on the blennioid fishes of western North America. Paps. Michigan Acad. Sci., Arts. & Letters, Ann Arbor 7:351–394.

———. 1952. Antitropical distribution of fishes and other organisms. Symposium on problems of bipolarity and of pantemperate faunas. Seventh Pacific Sci. Congr. (Pac. Sci. Assoc.). III:1–6.

———. 1960. The marine vertebrates of the outer coast. Baja California Symposium. Syst. Zool. 9:134–147.

———, AND A. B. RECHNITZER. 1958. A new fish, *Chaetodon falcifer*, from Guadalupe Island, Baja California, with notes on related species. Proc. California Acad. Sci. 29:273–313.

INTERNATIONAL UNION OF BIOCHEMISTRY. NOMENCLATURE COMMITTEE. 1984. Enzyme nomenclature, 1984. Academic Press, New York, New York.

KIRPICHNIKOV, V. S. 1981. Genetic bases of fish selection. Springer-Verlag, New York, New York.

LEVENE, H. 1949. On a matching problem arising in genetics. Ann. Math. Stat. 20:91–94.

LYNN, R. J., K. A. BLISS, AND L. E. EBER. 1982. Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-T, stability, dynamic height, oxygen, and oxygen saturation in the California current, 1950–1978. CALCOFI Atlas No. 30. Marine Life Research program, Scripps Institution of Oceanography, La Jolla, California.

MURRAY, S. N., M. M. LITTLER, AND I. A. ABBOTT. 1980. Biogeography of the California marine algae with emphasis on the southern California islands, p. 325–339. *In:* The Channel Islands: proceedings of a multidisciplinary symposium. D. M. Powers (ed.). Santa Barbara Museum Natural History, Santa Barbara, California.

NEI, M. 1972. Genetic distance between populations. Am. Nat. 106:283–292.

———, T. MARUYAME, AND R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. Evolution 29:1–10.

ORTON, R. D. 1989. The evolution of dental morphology in the Girellidae (Acanthopterygii: Perciformes), with a systematic revision of the Girellidae. Unpubl. Ph.D. diss., Univ. of California, Los Angeles.

OWEN, R. W. 1980. Eddies of the California current system: physical and ecological characteristics, p. 237–263. *In:* The Channel Islands: proceedings of a multidisciplinary symposium. D. M. Powers (ed.). Santa Barbara Museum Natural History, Santa Barbara, California.

PRESENT, T. M. C. 1987. Genetic differentiation of disjunct Gulf of California and Pacific outer coast populations of *Hypsoblennius jenkinsi*. Copeia 1987: 1010–1024.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Univ. Texas Publ. 7213:145–153.

SASSAMAN, C., R. M. YOSHIYAMA, AND J. D. S. DARLING. 1983. Temporal stability of lactate dehydrogenase-A clines in the high cockscomb, *Anoplarchus purpurescens*. Evolution 37:472–483.

SEAPY, R. R., AND M. M. LITTLER. 1980. Biogeography of rocky intertidal macro-invertebrates of southern California islands, p. 307-323. *In:* The Channel Islands: proceedings of a multidisciplinary symposium. D. M. Powers (ed.). Santa Barbara Museum Natural History, Santa Barbara, California.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the old-field mouse (*Peromyscus polionotus*). Stud. Genet. Univ. Texas Publ. 6:49–90.

SHAKLEE, J. B., C. S. TAMARU, AND R. S. WAPLES. 1982. Speciation and evolution of marine fishes studied by the electrophoretic analysis of proteins. Pac. Sci. 36:141–157.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometery: the principle and practice of statistics in biological research, 2d ed. W. H. Freeman and Co., San Francisco, California.

SOMERO, G. N., AND M. SOULÉ. 1974. Genetic variation in marine fishs as a test of the niche-variation hypothesis. Nature (London) 249:670–672.

STEPIEN, C. A. 1986a. Life history and larval development of the giant kelpfish, *Heterostichus rostratus* Girard. Fish. Bull. 84:809–826.

———. 1986b. Regulation of color morphic patterns in the giant kelpfish, *Heterostichus rostratus* Girard: genetic versus environmental factors. J. Exp. Mar. Biol. Ecol. 100:181–208.

———. 1987. Color pattern and habitat differences between male, female, and juvenile giant kelpfish. Bull. Mar. Sci. 41:45–58.

———. 1990. Population structure, diets, and biogeographic relationships of rocky intertidal fishes in central Chile: high levels of herbivory in a temperate system. *Ibid.* 47:598–612.

———. 1992. Evolution and biogeography of the Clinidae (Teleostei: Blennioidei). Copeia 1992 (in press).

———, M. GLATTKE, AND K. M. FINK. 1988. Regulation and significance of color patterns of the spotted kelpfish, *Gibbonsia elegans* Cooper. Copeia 1988: 7–15.

———, H. PHILLIPS, J. A. ADLER, AND P. J. MANGOLD. 1991. Biogeographic relationships of a rocky intertidal fish assemblage in an area of cold water upwelling off Baja California, Mexico. Pac. Sci. 45: 63–71.

SWANK, S. 1979. Population genetics and evolution of some intertidal fishes of the genus *Clinocottus*. Unpubl. Ph.D. diss., Univ. of Southern California, Los Angeles.

SWOFFORD, D. L., AND R. B. SELANDER. 1981. BIOSYS-1: a FORTRAN program for the comprehen-

sive analysis of electrophoretic data in population genetics and systematics. J. Heredity 72:281–283.

———, AND ———. 1989. BIOSYS-1 vers. 1.7: a computer program for the analysis of allelic variation in population genetics and biochemical systematics. Illinois Natural History Survey, Champaign, Illinois.

THORPE, J. P. 1983. Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation, p. 131–152. *In:* Protein polymorphism: adaptive and taxonomic significance. G. S. Oxford and D. Rollinson (eds.). Academic Press, London, England.

VALENTINE, J. W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol. Oceanogr. 11:198–211.

VAWTER, A. T., R. H. ROSENBLATT, AND G. C. GORMAN. 1980. Genetic divergence among fishes of the Eastern Pacific and the Caribbean: support for the molecular clock. Evolution 34:705–711.

WAPLES, R. S. 1986. A Multispecies approach to the analysis of gene flow in marine shore fishes. Unpubl. Ph.D. diss., Scripps Inst. Oceanogr., Univ. of California, San Diego.

———. 1987. A multispecies approach to the analysis of gene flow in marine shore fishes. Evolution 4: 385–400.

———, AND R. H. ROSENBLATT. 1987. Patterns of larval drift in southern California marine shore fishes inferred from allozyme data. Fish. Bull. 85:1–11.

WILKINSON, L. 1988. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois.

WILLIAMS, G. C. 1954. Differential vertical distribution of the sexes in *Gibbonsia elegans* with remarks on two nominal subspecies of this fish. Copeia 1954: 267–273.

WINANS, G. 1980. Geographic variation in the milkfish *Chanos chanos* I. Biochemical evidence. Evolution 34:558–574.

WRIGHT, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. *Ibid.* 19:394–420.

———. 1978. Evolution and the genetics of populations. Vol. 4. Variability within and among natural populations. Univ. of Chicago Press, Chicago, Illinois.

WYLLIE, J. B. 1966. Geostrophic flow of the California current at the surface and at 200 meters. CalCOFI Atlas No. 4. State of California, Marine Research Committee, La Jolla, California.

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