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# SOUTHERN CALIFORNIA ACADEMY OF SCIENCES



## 1995 Annual Meeting May 5-6 California State University, Fullerton

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### Sample Abstract

6"

MICROBIAL ACTIVITY IN THE DIGESTIVE TRACT OF THE HALFMOON, *Medialuna californiensis*. J. S. Kandel<sup>1</sup>, J. R. Paterek<sup>2</sup> and M. H. Horn<sup>1</sup>. <sup>1</sup>California State Univ. Fullerton, CA 92634 and <sup>2</sup>Agouron Institute, La Jolla, CA 92037.

We report the presence of a diverse microbial flora and of microbial fermentation products in the hindgut region of the halfmoon, *Medialuna californiensis*, a seaweed-eating fish from southern California coastal waters. Viable aerobic and anaerobic bacteria were found in all sections of the gut, but were of highest concentration ( $10^5$ – $10^8$ /ml) in the hindgut. Microscopy revealed vibrios, spirilla, rod-shaped bacteria and flagellated protozoa in the midgut and hindgut, but primarily vibrios and rods in the stomach and foregut. Acetic, isobutyric and butyric acids, the volatile products of microbial breakdown of carbohydrates, were found only in the hindgut, as was ethanol, a nonvolatile product. These results provide the first evidence for microbial fermentation and its possible contribution to the energy supply in a north-temperate herbivorous fish.

4"

## Cultural Change and Geographic Variation in the Songs of the Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*)

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*Abstract.*—The Belding's Sparrow is a subspecies of the Savannah Sparrow that occurs only in isolated patches of *Salicornia* marsh habitat between Goleta, California and El Rosario Lagoon, Baja California Norte. Song samples were obtained from 14 local populations during 1973 and 7 populations were resampled during 1987/88. Turnover in the element lexicon of each population was low. A few elements changed in their proportional occurrence rate. During the initial survey it was noted that certain song types were common among males at any one locality. After 15 or 16 years the most common (popular) types in some populations remain dominant. At other localities types have changed in popularity. Sequence comparison analysis of elements within songs was conducted to produce an objective inter-song dissimilarity matrix. This analysis revealed that song variation within local populations is much less extensive than among populations. The features used to define the original dialects remain distinctive of the local populations.

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Geographic variation in bird song often exhibits discontinuous variation with local populations of birds singing distinctive local variants of the species-specific vocalization. Past work on long-term temporal shifts in bird song have assessed the extent to which population-specific "dialects" have remained stable (McGregor and Thompson 1988). In the current study, I studied population-specific geographic patterns of song structure in the Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*). I conducted an initial study of the singing behavior in 14 populations of the Belding's Sparrow between 1972 and 1974 (Bradley 1977). Seven of the largest of these populations were re-sampled during the springs of 1987 and 1988.

The main focus of the current study is the analysis of shifts in the patterns of use of the specific song types within local dialect populations. At this scale song variation reflects patterns of cultural drift within a population rather than potential exchange among populations. Many of the specific song elements or complete song types that were recorded in 1973 were still being used in populations 15 or 16 years later. This study evaluates the extent to which the proportion of males using these song elements and complete song types have changed. Such changes in song-type popularity reflect the cultural 'fitness' of learned song variants. Samples from 7 different populations represent replicate natural experiments in cultural evolution.

In addition to analysis of cultural change within local populations, I used sequence comparison analysis to quantify song variation among populations. The

second goal of the study was to examine the hypothesis that clear discontinuities occur within the range of geographic variation. As a corollary of this hypothesis I aver that these discontinuities correspond to local populations and reveal a history of behavioral isolation.

The subject of this work is the Belding's Savannah Sparrow, a well-marked subspecies (*beldingi*) of a widespread species (*Passerculus sandwichensis*). Each population of the Belding's Sparrow is geographically distinct, inhabiting small patches of salt marsh along the coast of California and Baja California del Norte (Grinnell and Miller 1944; Bradley 1973; Massey 1977; Fig. 1). Savannah Sparrows of this subspecies have been considered permanent residents (Grinnell and Miller 1944; Garrett and Dunn 1981). There are very few reports of this distinctive subspecies outside of these salt marshes (Grinnell and Miller 1944), and there may even be a physiological restriction to dispersal beyond saline environments (Cade and Bartholomew 1959; Poulson and Bartholomew 1962). Belding's Sparrows exhibit better weight maintenance (Cade and Bartholomew 1959) and are more active (Poulson and Bartholomew 1962) when kept in captivity with sea water than with fresh water. If distinct discontinuities exist among the populations of Belding's Sparrows, they may be attributable to the isolation created by this subspecies' habitat specificity.

### Methods

During 1973, recordings were made with a Uher 4000 Report S recorder and a Uher M 512 microphone mounted on a 61 or 76 cm fiberglass parabolic reflector. During 1987 and 1988 recordings were made with a Marantz CP221 cassette recorder and a Sennheiser K3U microphone with an ME88 directional head. Copies of the 1973 recordings are on file in the Bioacoustics Archive of the Florida Museum of Natural History, Gainesville, Florida. Copies of the 1987-88 recordings are on file at the Borror Laboratory of Bioacoustics at Ohio State University, Columbus, Ohio. Recording methodology was similar for both samples. I recorded individual males by walking through the occupied habitat on one or two mornings and recording singing territorial males as I entered their small display territories. I did not retrace my path or record in the same area more than once. When recordings were made on more than one morning, separate areas of the habitat were sampled. This method sacrifices maximal sample size to insure that no individual was sampled more than once (Bradley 1977). Population estimates for these populations were between 16 pairs at Agua Hedionda Lagoon and over 2000 pairs at San Quintin Bay (Bradley 1973; Massey 1977). The song samples include recordings from about 29% of the individuals in each of these small local populations (median, Table 1). Long-term study (6 years) in conjunction with color banding has established that individual male Belding's Sparrows sing only one song type (Bradley 1977; Massey 1979).

Audiospectrograms were made on either Kay Elemetrics 6061b, 7029a, or DSP 5500 audiospectrographs using both narrow and wide band filter settings and 160-16000 Hz scale. A lexicon of all distinguishable song elements was made by examining these audiospectrograms (Bradley 1977). A song element is any acoustical feature of a song that is separated from others by a silent gap. The sequence for a particular song type was represented in the analysis (coded) by listing the element codes as they occurred in the songs (Bradley 1977; Bradley and Bradley

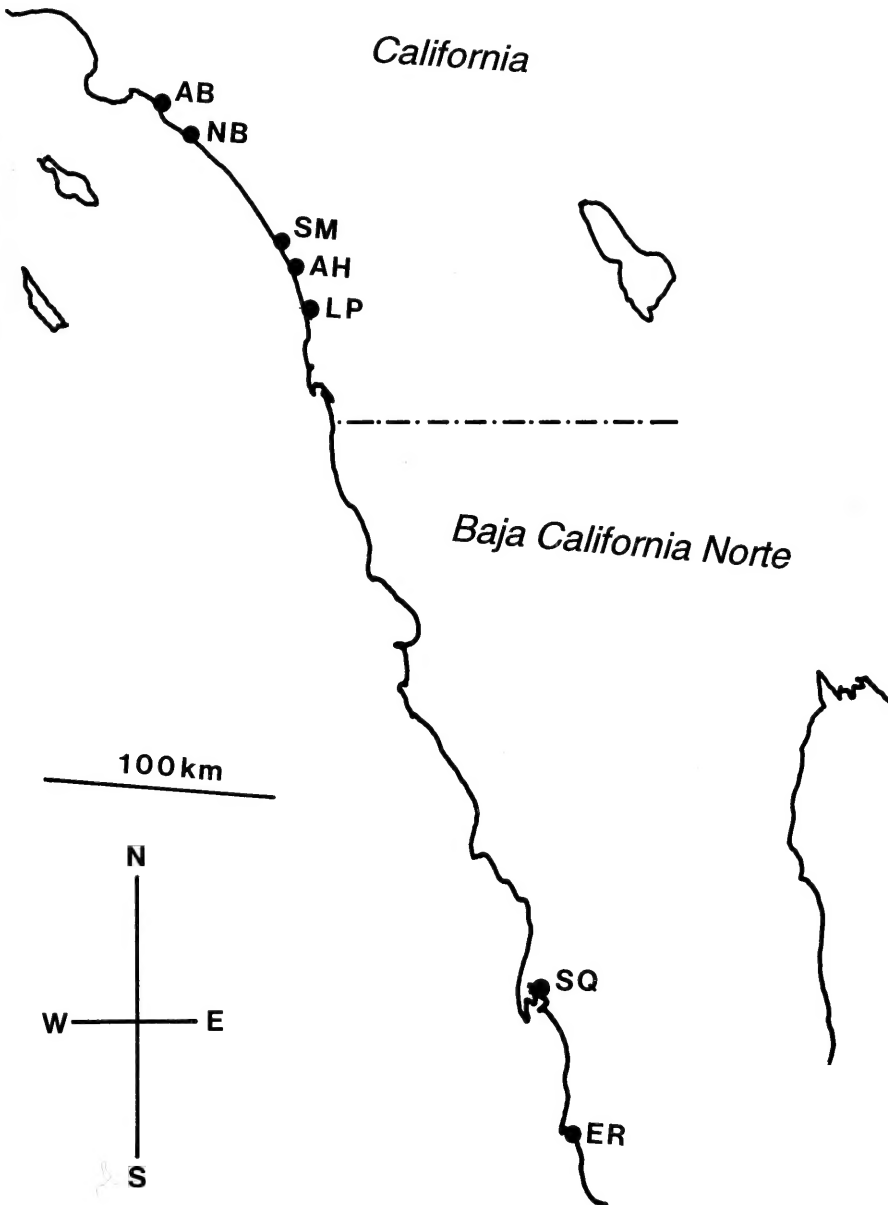


Fig. 1. A map of the 7 localities sampled during this study. Localities for which only small sample sizes were obtained are included on this map even though lexicon analyses could not be conducted for these sites. Coastline distances between the sites are in km. AB = Anaheim Bay, NB = Newport Bay, SM = Santa Margarita Estuary, AH = Agua Hedionda Lagoon, LP = Los Penasquitos Lagoon, SQ = San Quintin Bay, ER = El Rosario Lagoon.

1983). Rapid buzzes (>250 pulses/s) were classified as single elements. There was relatively little variation among individuals with respect to buzz fine structure, but buzzes differed in length. To include this variation in the analysis, the code for a buzz was repeated once for each 0.2 seconds of duration (0.2 s was the modal

Table 1. Summary of samples and song types for the 5 largest populations.

Locality (population) <sup>1</sup>	1973			1987/88		
	N <sup>2</sup>	Number of types	Dominance <sup>3</sup>	N	Number of types	Dominance
Anaheim Bay (267)	61	21	56%	70	31	34%
Newport Bay (83)	29	12	59%	24	15	38%
Santa Margarita (106)	29	13	41%	21	12	52%
Los Penasquitos (52)	21	12	48%	16	8	63%
San Quintin Bay (1000)	34	15	41%	31	20	29%
Total	174	73	50% <sup>4</sup>	162	86	39%

<sup>1</sup> Estimated number of breeding pairs from Massey (1979), estimate for San Quintin from Bradley (1973).

<sup>2</sup> Number of males recorded.

<sup>3</sup> Percent of males singing one of the three most common song types.

<sup>4</sup> Based on the 3 most common song types from each locality.

length of the shortest single buzz phrase). Patterns of similarity among the song elements were used to construct an inter-element dissimilarity matrix (Bradley and Bradley 1983).

All of the elements taken together comprise a song type, sometimes referred to as a theme or motif by other authors. The general song structure of Belding's Sparrows is described in detail elsewhere (Bradley 1977), but I will review the terminology briefly. The song is composed of a number of similar introductory elements followed by a series of short elements in a variety of patterns. The second half of the song is composed of a buzz phrase composed of relatively long buzzes as well as intervening short elements, and finally there is a terminal flourish. The terminal flourish follows the last buzz in the song and is short (1 to 5 elements, <0.3 s) and relatively invariant within a population. Chew (1981) employed a slightly different nomenclature for the sequence of song segments in Canadian populations of this species including an introductory (A) section that corresponds to my introductory elements; the note complexes that follow are classified by Chew as (B) and transition sections (C); the buzz section is referred to as the trill section (D); and finally the terminal flourish (not always present in Canadian songs) is referred to as the (E) section. The main difference between Chew's and my approach is that I focus on finer-scale individual element sequences while he uses section sequences in his analysis.

For the present study each unique sequence-list corresponds to one unique song type. Each male sang only one song type. The only exceptions were for the minor variation which occurred within a song type in the number of repetitions of the introductory note or the exact length of a buzz phrase. For males that sang songs with different numbers of introductory notes, the longest song was used to represent that male. The song type of each male in the sample was coded as a sequence of elements (based on the lexicon). The song sequences were compared directly and with a series of computer programs (BELDINGS) developed for this purpose (Bradley and Bradley 1983). These programs use an optimal-matching algorithm for the sequence comparison that generates an inter-song dissimilarity measure (Bradley and Bradley 1983). Briefly, this method compares the coded sequences representing any two songs and calculates the minimum number of changes (ad-



ditions, deletions and substitutions) necessary to produce an identical match. The numerical value of a substitution is weighted by the acoustical similarity of the two song elements involved. This method provides a sensitive and objective measure of song similarity. For a detailed description of the method consult Bradley and Bradley (1983).

A randomization test analogous to ANOVA was used to compare differences among individuals within a population and between populations and sampling years (Sokal and Rohlf 1981). For this randomization test, the test statistic was the ratio of the mean within-group song dissimilarity to the mean between-group song dissimilarity. Discriminant function analysis was used to produce a model to assess the distinctiveness of the song variation among populations. Pearson product-moment correlation analysis was used to compare mean song dissimilarity and geographic separation among populations.

Only the 5 localities represented by the largest sample sizes were analyzed for variation in the occurrence of song type variants and shifts in the element lexicon. The other two localities' samples (Agua Hedionda Lagoon  $N = 10$  (1973) and 3 (1988), El Rosario Lagoon  $N = 11$  (1973) and 16 (1988)) were too small to warrant such analyses. A Chi-square test of goodness-of-fit was used to assess the similarity of occurrence patterns of individual elements between the sampling years for each population. One-way ANOVA was used to assess variability among two song pattern variables (number of elements per song type, number of element types per song type). A simple index of similarity ( $I$ ) was used to compare the lexicon patterns among populations. The index  $I = 2c/(a + b)$  where  $a$  and  $b$  are the number of different element types in each population and  $c$  is the number of elements common to both populations.

## Results

### *Occurrence of Song Types*

Although patterns of variation within populations are less dramatic than between populations, clear differences exist among the individuals within a population. These differences are primarily in the number and form of elements between the introductory notes and the buzz sections of the songs. The number of different song types represented by recordings from each sampling locality varied from 8 to 31 and generally reflects the number of males recorded (16 to 70, Table 1). In each population there are certain song types that are shared by many males (Fig. 2). In the 1973 sample 50% of males sang one of the three dominant song types at each locality (Bradley 1977). The 1987/88 data reveal that 39% of males sang one of the three dominant types (Table 1). If the occurrence of song types merely reflected random sampling one would expect 21% of the males from the 1973 sample and 17% of the males from the 1987/88 sample to sing three types (Table 1). Most song types have changed in popularity between samples (Table 2). A sum of all individuals singing the most popular song type in 1973 across these 5 populations is 40 of 174 or 23% of the sample. Only 15 of 162 (9%) sang these same types in the 1987/88 sample. In only 2 of the 7 populations did the rank 1 song remain the most popular song type. In 2 of the remaining 5 populations the new first rank position was occupied by birds singing the previous rank 2 song. At San Quintin Bay the third most popular type in 1973 became the most popular

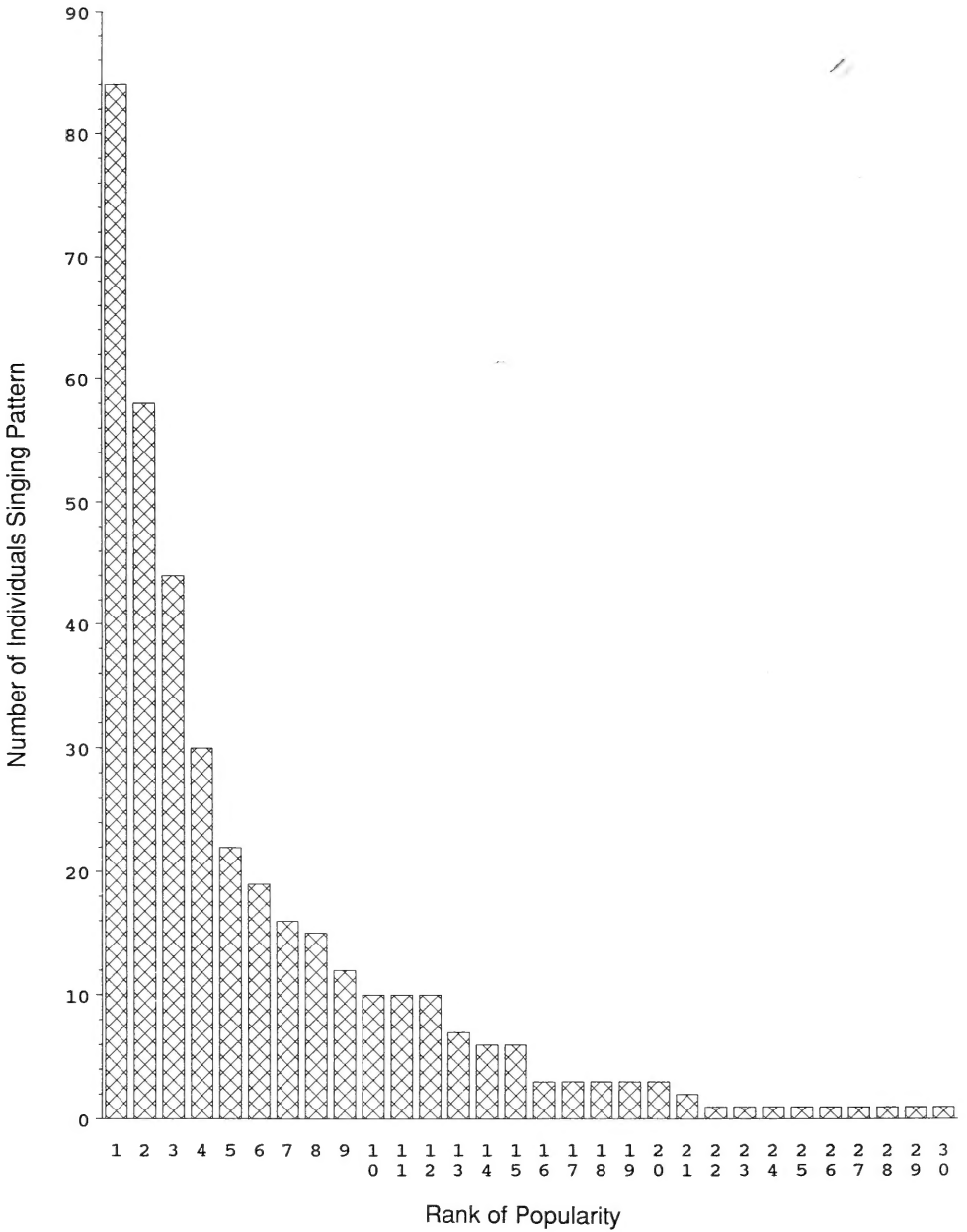


Fig. 2. A histogram of the number (vertical axis) of the individual Belding's sparrows that sang songs with the rank of popularity indicated (horizontal axis). The total sample is composed of 336 birds singing 159 song types. Each of the seven populations is evaluated twice, once for 1973 and once for 1987 or 1988. Rank 1 songs from all populations are combined in the first bar, rank 2 in the second bar, etc. If songs were distributed evenly and randomly one would predict that only 28 individuals would sing the most popular (rank 1) songs.

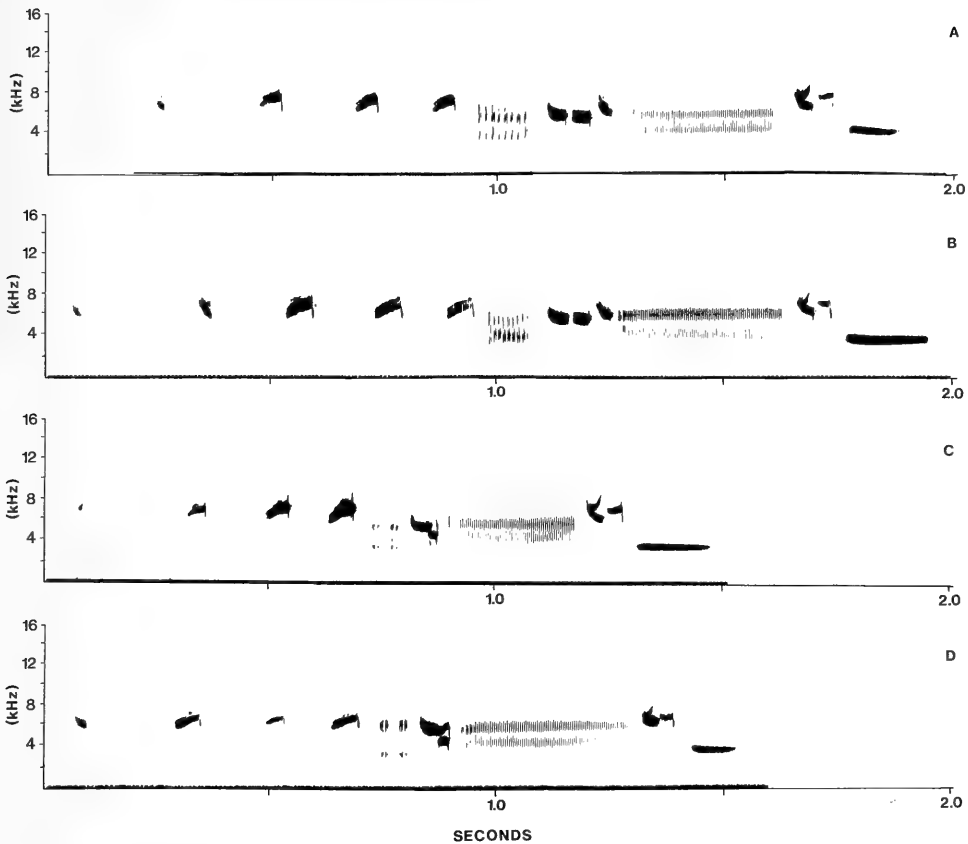


Fig. 3. Examples of popular songs that retained a similar form in subsequent sample. The rank 1 song at Anaheim Bay in 1973 (A), the same song type remained as rank 1 in 1987 (B). The songs A & B have a dissimilarity value of 0.23. The rank 2 song at Anaheim Bay in 1973 (C) was used by only two individuals in 1987 (D), dropping to rank 17. The songs C & D have a dissimilarity value of 0.17. In contrast the average of the four dissimilarity measures among different songs in this figure is 0.40.

type in 1988. For the remaining 2 populations a new song type rose to first rank. Nevertheless, some of the dominant song types in 1973 were still popular in their respective populations in the 1987/88 sample (Table 2, Fig. 3). For example the single most common type (rank 1) recorded at Anaheim Bay in 1973 was also the most common in 1987. In contrast the rank 2 song from 1973 at Anaheim Bay became rare in 1987 and was sung by only two males (rank 17).

Despite changes in popularity, the fact that many song types remained unchanged indicates that song types are often copied intact. Examining all song types (not just the dominant ones) reveals that relatively few types were shared between samples (Table 3). Nevertheless these 12 shared types represent 19% of the individual males in the 1987/88 sample. In addition to invariant song types, some song types changed only slightly (Fig. 4A, B). In other populations very different song types gained popularity (Fig. 4C, D).

Table 2. Summary of the shifts in dominance of song types between samples.

Locality	1973 most popular 3 types			1987/88 use of same 3 types		
	No. birds (rank)			No. birds (rank)		
Anaheim Bay	18 (1)	8 (2)	6 (3)	13 (1)	2 (17)	0
Newport Bay	7 (1)	6 (2)	4 (3)	0	6 (1)	0
Santa Margarita	5 (1)	4 (2)	3 (3.5) <sup>1</sup>	0	0	1 (16)
Agua Hedionda	3 (1)	2 (2.5) <sup>1</sup>	2 (2.5) <sup>1</sup>	3 (1)	0	0
Los Penasquitos	4 (1)	3 (2)	2 (3.5) <sup>1</sup>	0	0	0
San Quintin	6 (1)	5 (2)	4 (4.5) <sup>2</sup>	2 (22)	0	8 (1)
El Rosario	6 (1)	4 (2)	1 (3)	0	15 (1)	0

<sup>1</sup> The use of a fractional rank indicates a tie between two ranks.

<sup>2</sup> Four song types tied for third rank.

### *Changes in Element Lexicon*

Initial classification produced a lexicon of 46 distinct element types from the 5 populations studied in detail here. This lexicon is largely a subset of the one illustrated in Figures 1 and 2, p. 62 and 64 in Bradley (1977). A total of 9 elements present in the 1973 songs are absent among the 1987/88 songs. Five new elements appear in the recent sample. This appears to represent a 30% degree of "turnover" in song elements when expressed as the total number of changes divided by the combined lexicon (Table 4). This figure is a distortion because most of the lost or gained elements were sung by very few individual birds. Of the 9 element types lost, 8 were sung by 3 or fewer individuals. Likewise, of the new 5 elements, 3 were sung by 3 or fewer individuals. When the estimate of turnover is "weighted" by considering the frequency of occurrence of elements there appears to be a relatively minor change in the overall lexicon of just 3% (Table 4). In other words, the only changes in the lexicon lists for the two samples were among relatively rare elements. Sampling error may contribute to this turnover estimate; if some elements which were actually present were missed, the real turnover rate would be even lower. What about element occurrence between years within each locality? Chi-square analysis reveals that the proportional frequencies of the elements

Table 3. Song types shared in both 1973 and 1987/88 samples for the 5 largest populations sampled.

Locality	N <sup>1</sup>	Number of shared patterns <sup>2</sup>	Percent of birds in 1987/88 sample singing shared patterns <sup>3</sup>
Anaheim Bay	47	5	26
Newport Bay	25	2	8
Santa Margarita	24	1	19
Los Penasquitos	19	1	6
San Quintin Bay	32	3	19
Total	147	12	19

<sup>1</sup> Number of different song types in both samples combined.

<sup>2</sup> Number of birds in 1987/88 singing song types that are identical to song types recorded during 1973.

<sup>3</sup> The number of individual males that sang one of the shared types as a percentage of the 1987/88 sample.

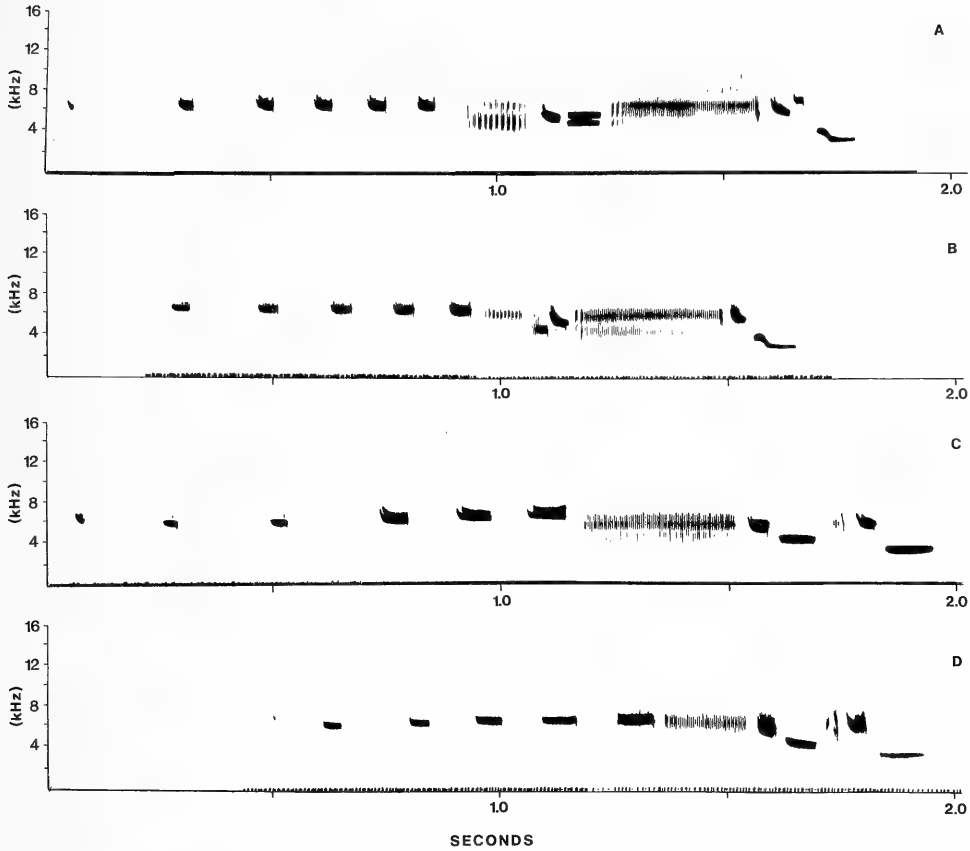


Fig. 4. Examples of popular songs that were replaced in the population by new or previously unpopular types. The most popular song type at Los Penasquitos in 1973 (A) is slightly different from the most popular type recorded at that locality in 1988 (B). The songs A & B have a dissimilarity value of 0.61. The most popular song type at El Rosario in 1973 (C) is slightly different from the rank 1 song in 1988 (D). This new popular song (D) was the second most popular type at El Rosario in 1973. The songs C & D have a dissimilarity value of 0.61. The average of the four dissimilarity measures among different songs in this figure is 0.71.

differed significantly between years in 4 of the 5 population samples analyzed ( $P < 0.01$  for each). Only the Anaheim Bay samples were indistinguishable. This reflects the changing patterns of song-type popularity. The Anaheim Bay population differs from the other four in that the single most popular song type at Anaheim Bay in 1973 was still the most popular in 1987.

#### *Geographic Variation*

Variation among populations involves the form of song elements (lexicon) as well as the sequence and general form of song arrangement. The terminal flourish is the most distinctive feature of songs shared by individuals at each locality that differs among localities. Song dissimilarity can vary between 0.0 (identical songs) to 1.0 (no similarity). Mean values calculated from my sample vary from 0.047 (within Agua Hedionda Lagoon, 1988) to 0.854 (between El Rosario Lagoon in

Table 4. Summary of changes to the element lexicons for the 5 largest samples.

Locality	1973 lexicon	1987/88 lexicon	Elements lost	New elements	Turnover <sup>1</sup>	Weighted turnover <sup>2</sup>
Anaheim Bay	23	21	3	1	9%	1%
Newport Bay	23	17	9	3	30%	6%
Santa Margarita	18	14	5	1	33%	3%
Los Penasquitos	15	16	1	2	10%	4%
San Quintin Bay	17	15	4	2	19%	2%
All localities	41	35	9	5	30%	3%

<sup>1</sup> The number of changes divided by the total lexicon for both samples combined.

<sup>2</sup> The number of occurrences of changed elements divided by the number of occurrences of unchanged elements. This value effectively weights the change by frequency of element use.

1973 and Newport Bay in 1988). The sequence comparison analysis reveals that variation among songs between each population of Belding's Sparrows is significantly greater than song variation within the populations for both the original (1973) and subsequent (1987/88) song samples ( $P < 0.001$ , Table 5).

Three separate discriminant function analysis models were created based on the sequence comparison results. One model was created for each sample separately, and a third model was built for the two samples combined. The model for the 1973 data correctly assigned 95% of individuals to the correct group (the population where they were recorded). The 1987/88 model correctly assigned 100% of individuals. The model based on songs from both samples combined correctly assigned 99% of individuals to the a-priori groups. Thus variation in song between years and between individuals is relatively minor compared to variation among recording localities.

Mean song dissimilarity among populations that are relatively near each other

Table 5. Song similarity as assessed by sequence comparison analysis among individuals within each locality and between localities. The values in the table are mean dissimilarity measures. This measure approaches zero for identical songs.

Locality	1973		1987/88	
	N <sup>1</sup>	Within locality	N	Within locality
Anaheim Bay	1830	.328	2415	.338
Newport Bay	406	.333	276	.286
Santa Margarita	406	.332	210	.290
Agua Hedionda	45	.256	3	.050
Los Penasquitos	210	.347	120	.348
San Quintin Bay	561	.391	465	.296
El Rosario	55	.151	120	.086
		Within Groups		
All localities	3513	.336	3609	.316
		Among Groups		
All localities	15,402	.534**	12,681	.712**

\*\* Indicates that these values are different from within groups values at  $P < 0.001$ .

<sup>1</sup> Number of comparisons or one half of a symmetrical matrix excluding diagonal elements (self comparisons).

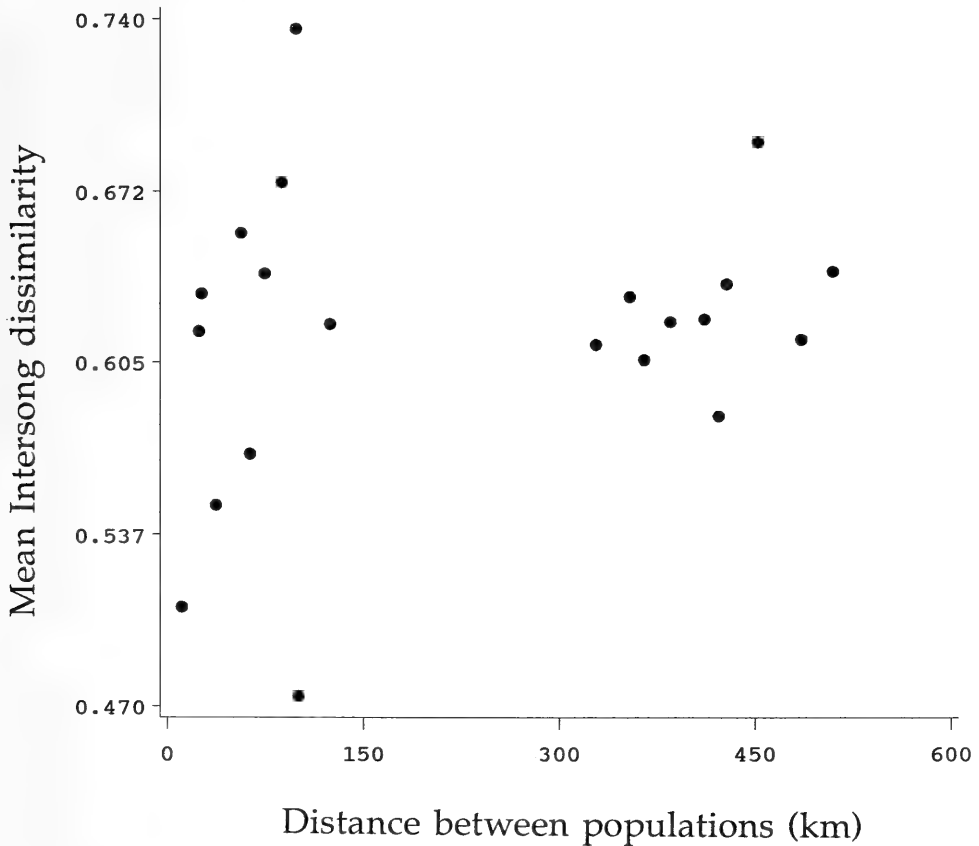


Fig. 5. The relationship between the mean song dissimilarity (vertical axis) measured with sequence comparison for each pair of populations with the map distance (horizontal axis) between these localities. Data from both 1973 and 1987/88 samples are included. Dissimilarity measures can range from 0.0 (identical songs) to 1.0 (no similarity).

was either large or small, but distant populations nearly always have distinctly different songs (Fig. 5). All of the comparisons where the localities were separated by more than 160 km exhibited a mean song dissimilarity of 0.575 or greater (Fig. 5). I found no correlation between the mean song dissimilarity measure among populations and the geographic distance separating them ( $r = 0.22$ , ns; Fig. 5, Fig. 1).

Inspection of the audiospectrograms reveals that the distinctive terminal flourish, characteristic of each population in 1973 (Bradley 1977), has remained unchanged for most populations (Fig. 6). The most typical form of terminal flourish in 1973 was still dominant in 1987/88 in 6 of the 7 populations (Fig. 6). The sample from El Rosario Lagoon in 1973 contained two common terminal flourishes. The less common form which was used by only 4 of 11 males recorded in 1973 was present in the songs of all 16 males recorded in 1988.

There were no significant differences among populations with respect to the number of elements in the song types representative of each ( $F = 1.11$ ,  $df\ 4,154$ , ns). Internal song-type complexity as revealed by the number of different element

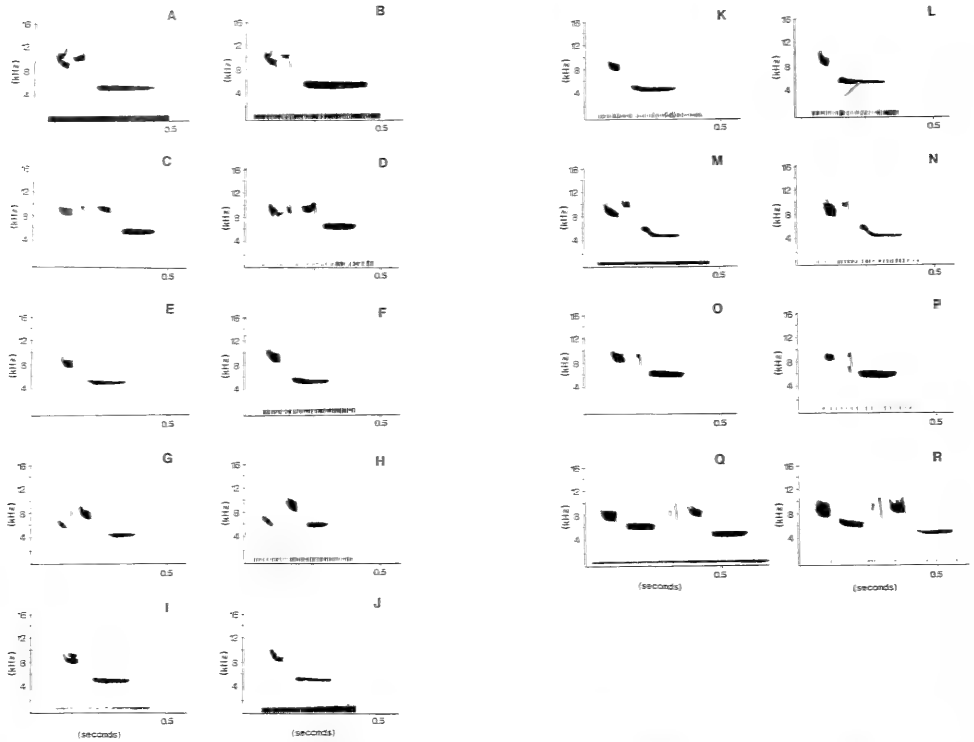


Fig. 6. Examples of the typical terminal flourish for each population for both sampling periods. The terminal flourish is a complex of song elements that concludes the song and occurs just after the buzz phrase (Bradley 1977). A) Anaheim Bay 1973, B) Anaheim Bay 1987, C) Newport Bay 1973, D) Newport Bay 1987, E) Santa Margarita Estuary 1973 (2-element form), F) Santa Margarita Estuary 1988 (2-element form), G) Santa Margarita Estuary 1973 (4-element form), H) Santa Margarita Estuary 1988 (4-element form), I) Agua Hedionda Lagoon 1973, J) Agua Hedionda Lagoon 1988, K) Los Penasquitos Lagoon 1973 (2-element form), L) Los Penasquitos Lagoon 1988 (2-element form), M) Los Penasquitos Lagoon 1973 (3-element form), N) Los Penasquitos Lagoon 1988 (3-element form), O) San Quintin Bay 1973, P) San Quintin Bay 1988, Q) El Rosario Lagoon 1973, R) El Rosario Lagoon 1988.

types per song did vary significantly between populations ( $F = 18.96$ ,  $df\ 4,154$ ,  $P < 0.001$ ). Anaheim Bay songs contain more variety ( $\bar{x} = 10.7$  element types/song type), while Santa Margarita and Los Penasquitos contain less ( $\bar{x} = 7.7, 7.9$  element types/song type respectively). For each population the lexicon similarity index was highest when the 1973 sample was compared to the later sample from that locality, the mean index of similarity (I) for the 5 such comparisons equals 0.83. There was no relationship between the index of similarity computed between the two samples from a locality and its population size ( $r = 0.00$ , ns), or sample size ( $r = +0.07$ , ns). Thus shifts in the lexicon do not seem to be related directly to population size. Comparisons among the populations reveal that neighboring populations share somewhat similar element lexicons. The Spearman rank correlation of the index of similarity with distance between populations was  $-0.76$  ( $P < 0.01$ ). This relationship does not appear to be linear (Fig. 7).



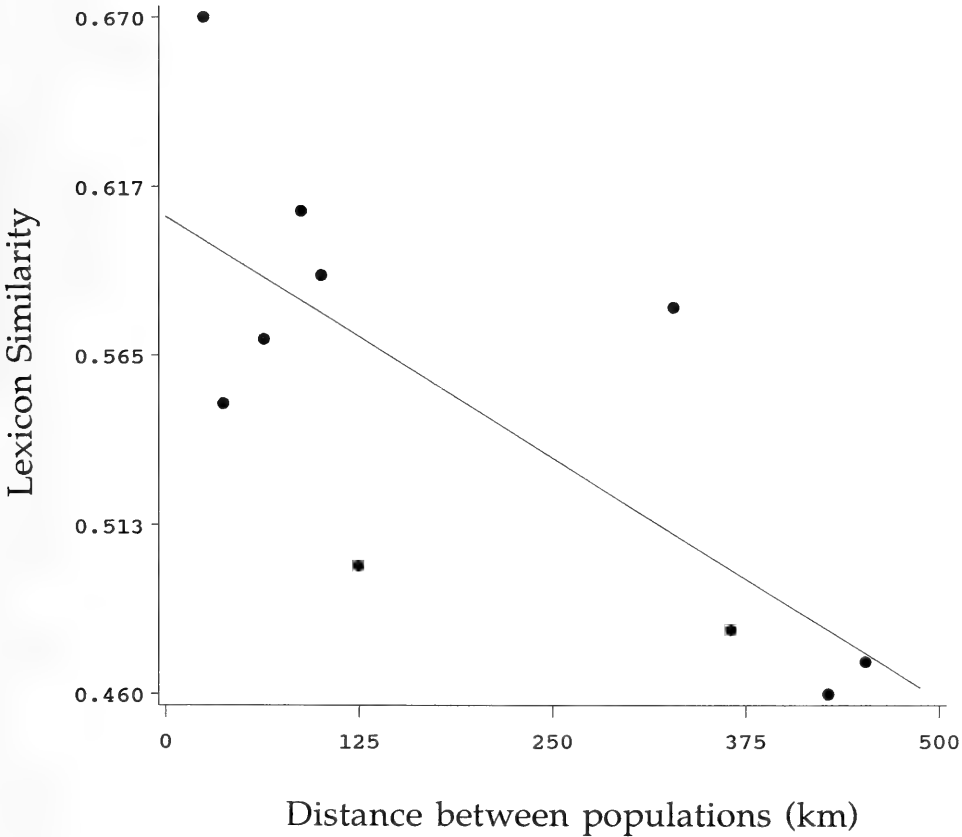


Fig. 7. The relationship between the similarity of the lexicon lists (vertical axis) of a pair of populations with the map distance (horizontal axis) between them. Data from the 5 largest populations for both sampling periods are included. The line represents the regression line for this relationship ( $r^2 = 0.40$ ). The index of similarity can range from 0.0 (no similarity) to 1.0 (identical lexicon lists).

### Discussion

The patterns of song variation among Belding's Sparrow populations is somewhat different from that described for the eastern Canadian populations studied by Chew (1981). Chew indicates that variation in the trills (=buzzes of this study) characterized the regional populations. In Belding's Sparrows variation in buzz phrases was relatively minor. Chew found terminal song sections were absent in 20% of the Savannah Sparrows that he recorded (Chew 1981). The terminal sections of Canadian Savannah Sparrows (Chew 1981) were much less complex and shorter than the corresponding parts of Belding's Sparrow songs. The sequences of song sections were consistent among Belding's Sparrow populations and varied significantly among the Canadian populations studied by Chew (1981). Two factors may explain these differences; first, Chew used a different scale for his grammatical analyses than I employ in the sequence comparison analysis. Chew (1981) compares sequences of song sections while I compare sequence of individual song elements. Second, the populations studied by Chew were separated

by much greater geographic distances than the populations of Belding's Sparrows. One clear similarity between these two studies is that a few songs were used by the majority of males at any one locality. Among Canadian populations 61–80% of the individuals sang one of three song types (Chew 1981, p. 710). Among Belding's Sparrow populations 34–63% shared the three most popular types (Table 1).

Variation within populations of the Belding's Sparrow is characterized by a few popular song types used by many of the singing males. Most populations that I studied experienced a shift in the proportional use of song types between 1973 and 1988. If juvenile males imitate their father's song as is the case in a few species (Immelmann 1969; Nicolai 1959; Gibbs 1990; Zann 1990) these popularity shifts might represent an indirect measure of the reproductive success of their fathers. Gibbs (1990) has demonstrated that song variation is related to reproductive success in *Geospiza fortis* and suggests that cultural evolution and biological evolution reinforce each other. If young birds model their songs after other (unrelated) individuals in the population, shifts in song-type use may simply reflect shifts in the songs that were frequently copied as has been demonstrated in the Saddleback, *Philesturnus carunculatus rufusater* (Jenkins 1977) and other species (Petrinovich 1988; Payne and Payne 1993). Distinguishing between these two alternatives (learning from father or neighbors) would be difficult in the Belding's Sparrow because large groups of neighboring males sing exactly the same song type. In one case a wild Savannah Sparrow learned the song of a White-crowned Sparrow (Cooper and Murphy 1985) so it is clear that they are capable of learning songs different from that of their father. Laboratory work suggests that birds learn songs from individuals with whom they interact regularly, or which are dominant in a particular setting (Baptista and Petrinovich 1984; Petrinovich 1985; Slater et al. 1988). In most of the Belding's Sparrow populations that I studied, males with similar songs are spatially clumped (Bradley 1977). In studies of color-banded males there was no evidence of males changing their songs or imitating the songs of their neighbors for periods up to 4 years (Bradley 1977; Massey 1979). The type of songs which are common in local populations (Table 2) may reflect the fact that males in some song groups exert a disproportionate influence on the process of song learning. These song groups expand at the expense of others. Song groups are not completely homogeneous, some individuals singing different song types can be found within them. This pattern may reflect the settlement patterns of individual males.

Local song groups and dialects in other species may be the result of both philopatry and imitation of the song variants used by resident birds. Work on Indigo Buntings, *Passerina cyanea*, has shown that young males arriving to breed for the first time copy the songs of established territory holders with whom they interact (Payne 1981b, 1983; Payne and Payne 1993). Because such imitation is mediated by direct interactions among individuals it has been dubbed the "social adaptation model" (Payne 1981a). The pattern that results from this social interaction is a series of small neighborhoods of 2–12 males singing similar songs (Payne et al. 1981). Strong social interactions were influential in determining which song young White-crowned Sparrows (*Zonotrichia leucophrys*) learned in captivity (Baptista and Petrinovich 1986) and in the wild (Baptista and Petrinovich 1984; Baptista 1985; Petrinovich and Baptista 1984). Similar learning patterns were

Table 6. Comparison of geographic distance and sequence-comparison song dissimilarities among the five large population samples of Belding's Sparrows. The lower half of the table are the coastline distances (km) and the upper half are the mean song dissimilarities for both sampling periods combined. Dissimilarity measures can range from 0.0 (identical songs) to 1.0 (no similarity).

	AB	NB	SM	LP	SQ
Anaheim Bay (AB)	—	.68	.71	.69	.67
Newport Bay (NB)	24	—	.66	.65	.68
Santa Margarita (SM)	87	63	—	.65	.71
Los Penasquitos (LP)	124	100	37	—	.66
San Quintin Bay (SQ)	432	428	365	328	—

observed in wild populations of this species (Baptista and Morton 1988; DeWolfe et al. 1989). Saddlebacks acquire songs similar to the territorial neighbors with which they have direct social contact, thus forming local song neighborhoods or song groups (Jenkins 1977).

Song variation within Belding's Sparrow populations is relatively minor when compared to variation among the populations (Table 5). Beyond this simple pattern, correlation analysis indicates that there is no cline in vocal similarity among adjacent populations at the level of entire songs (Fig. 5). It is surprising that the two pairs of close populations (Newport Bay—Anaheim bay 24 km and Los Penasquitos—Santa Margarita 37 km) share song sequences that are no more similar than some of the most widely separated populations (Table 6). The Anaheim Bay and Newport Bay populations have been separated by extensive urban development (except immediate beach area) for a relatively long period. This is not the case between Santa Margarita Estuary and Los Penasquitos Lagoon where coastal development is much less extensive, even today. This result reinforces my interpretation that all of these populations have been isolated for many generations.

Mundinger (1982) suggests that analysis of the patterns of geographic distribution of song elements (isogloss analysis) is an effective method of assessing the evolution of microgeographic variation in vocal behavior. Comparisons of the lexicon of elements among populations in Belding's Sparrows yield a weak clinal geographic pattern (Fig. 7). I consider the imitation of song elements between birds from different source populations to be a form of behavioral exchange of cultural memes (sensu Dawkins 1976) analogous to gene exchange. I conclude that exchange of memes among populations of Belding's Sparrows has probably involved incorporation of new elements rather than entire songs.

The discovery that little meme exchange has occurred among the populations of the Belding's Sparrow implies that these populations have either been very isolated from each other, or that subsequent behavioral divergence has been relatively rapid. Estimates of annual survival and population turnover are important to an assessment of the significance of shifts in occurrence of song types between these two samples. Massey (1979) in a six year color banding study estimated that annual adult male survival was about 64%. This estimate is at the high end of those published for this species (Wheelwright and Rising 1993). Using the formula in Gill (1990) the mean life expectancy based on this estimate would be 2.6 yr. Mortality may drop in individuals older than 5 years (Wheelwright and

Rising 1993). Another factor indicates that the actual life expectancy is probably lower; there is much higher mortality among first year male Savannah Sparrows (Wheelwright and Rising 1993). I conclude that there have probably been three to four population turnovers in the 15 years between the two samples in this study. Re-sampling indicates that relatively few changes in songs have occurred during this period. McGregor and Thompson (1988) reviewed the evidence for stability in song dialects and concluded that stasis has been documented for periods ranging from 6 to 28 years among 7 species of oscine passerines. Cultural shifts over relatively short periods occurred among Indigo Buntings, yet a few song types persisted for 15 years (Payne et al. 1981). The boundaries between song dialects have shifted position in some populations of White-crowned Sparrows (Trainer 1983), indigobirds (*Vidua*) (Payne 1985) and European Starlings (*Sturnus vulgaris*) (Adret-Hausberger 1986).

Bowman (1979) demonstrated that a relationship exists between song structure and the physical acoustical environment in Galapagos finches. Gish and Morton (1981) have argued that geographic variation in the songs of the Carolina Wren are the result of selection for songs which possess physical properties appropriate for transmission in the particular acoustical environment of the geographic locality. Handford (1988) attributed a significant portion of the geographic variation in *Zonotrichia capensis* songs to adaptation to the acoustical propagation properties of the local vegetation. Thus it is possible that patterns of geographic variation in bird song reflect differences in the local habitat. Adaptation to local habitat acoustics seems to be an unlikely explanation for dialects in the case of the Belding's Sparrow for two reasons. First, all populations of this sparrow occupy coastal salt marsh dominated by the same 2 or 3 plant species (Bradley 1977) with virtually identical topography, vegetation physiognomy and climate. Thus these populations probably share the same selective environment with respect to song degradation. Second, the features of the fine structure of the songs that vary among Belding's Sparrow populations do not differ in ways that would likely affect their transmissibility. The differences are mainly in the arrangement of elements and variants of elements which share the same frequency and amplitude envelopes. The songs also share the same general acoustical pattern (Bradley 1977).

Some authors have considered geographic variants as selectively neutral epiphenomena that are a consequence of imperfect song learning (Andrew 1962; Wiens 1982). Marked discontinuities in singing behavior have been implicated as potential behavioral isolating mechanisms (Marler and Tamura 1962; Nottebohm 1969; Baker 1975; Baker and Cunningham 1985). The available genetic evidence for such isolation has been challenged (Zink and Barrowclough 1984; Hafner and Petersen 1985; Loughheed and Handford 1992). Others have shown that song learning may occur after dispersal, which would presumably dilute the effectiveness of local songs as markers of local origin (Kroodasma 1974; Jenkins 1977; Baptista and King 1980; Baptista and Morton 1982; Baptista and Petrinovich 1984; McGregor et al. 1988). In separate reviews, Payne (1981a) and Baptista (1985) have concluded that geographic variation in song is a product of the social milieu and that little evidence for an behavioral-isolation function exists. It has also been shown that mate choice was unrelated to song type of potential mates in a mixed-dialect population (Chilton et al. 1990). In the case of the Belding's Sparrow, isolation may result from geographic separation combined

with habitat specificity and behavioral isolating mechanisms may be of relatively minor importance.

Even if the songs themselves do not serve to enhance isolation of local populations the patterns may provide us with a record of historical contact (Baker and Thompson 1985). Belding's Sparrow populations exhibit geographic discontinuities in song structure, as well as little evidence of similarity among adjacent populations. The conclusion that I draw from the analysis of these song types is that there has been relatively little meme exchange between the isolated populations of Belding's Sparrows.

Rothstein and Fleischer (1987) provide an alternate hypothesis for the maintenance of song dialects that does not involve isolation. Their hypothesis avers that males singing local song dialects are providing an "honest signal" of local origin which may be used by females in selecting mates. Familiarity with local song types may also enhance efficiency in assessment of territorial intrusion. Morton (1982) has suggested a mechanism for this is comparison of a song to the stored memory of a familiar undegraded song. Thus familiar local song variants may be exploited by birds for their information value in both social and physical-acoustical ways.

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**Helminth Parasites of Some Southern California Fishes with a  
Redescription of *Proctoeces magnorus* Manter, 1940  
(Digenea: Fellodistomidae) and Description of  
*Choanodera moseri* sp. n.  
(Digenea: Apocreadidae)**

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*Abstract.* — Approximately 1400 marine fishes collected in and around Los Angeles and Long Beach Harbors were examined for parasitic helminths between May 1979–March 1992. Ten families of helminth parasites were collected from 18 species of southern California marine fish that represent new host-parasite records. A new species is described, *Choanodera moseri* sp. n., as well as a redescription of *Proctoeces magnorus* Manter, 1940.

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Parasites of southern California marine fishes were surveyed from 1975–1979 (Dailey et al. 1981). During this study, 2268 fishes were examined, primarily for nematodes of the two genera *Anisakis* and *Pseudoterranova* (*Phocanema*). In 1983, Love and Moser published a check list of parasites of marine fishes for the western United States that included southern California species.

During the present study, parasitic helminth were recovered from a total of approximately 1400 marine fishes captured between May 1979–March 1992, in and around the waters of Los Angeles and Long Beach harbors. The results of this investigation, which includes new host-parasite records, a redescription of *Proctoeces magnorus* Manter, 1940 (Digenea: Fellodistomidae) and an original description of a new species of *Choanodera* (Digenea: Apocreadidae) are presented in this paper.

#### Methods

Fish were collected by trawl aboard the R/V *Yellowfin* for examination by students enrolled in general parasitology at California State University, Long Beach (CSULB). Fish were identified using Miller and Lea (1972), sexed, measured, eviscerated (gills and gut), and packed on ice immediately after capture. Trematodes were fixed in alcohol-formalin-acetic acid (AFA), stained in Semichon's carmine, dehydrated in ethyl alcohol, cleared in xylene, and mounted in balsam resin. Nematodes were killed in hot 70% ethyl alcohol, cleared in glycerin, and mounted in glycerine jelly. Drawings were made with the aid of a drawing tube. Measurements are in micrometers unless otherwise indicated, with ranges followed by means in parentheses.

#### Results

Eleven families of helminth parasites were collected from 18 species of fishes in southern California waters that represented new host-parasite records (Table



1). Six specimens of *Proctoeces magnorus* were recovered from two California sheephead, *Semicossyphus pulcher* (Ayres) and 11 specimens of *Choanodera moseri* sp. n. were found, four and seven respectively from two barred sand bass, *Paralabrax nubilifer* (Girard) and two ocean whitefish, *Caulolatilus princeps* (Jennyns).

#### Description

##### *Choanodera moseri* sp. n.

(Fig. 1)

*Choanodera moseri* sp. n. Apocreadidae Skrjabin, 1942. The following description based on 11 specimens (2 adults, 9 immature).

*Specific diagnosis.*—Body elongate, thick, with widest part at level of acetabulum. Anterior part of worm only slightly tapering, posterior end rounded. Length 0.601 to 2.052 mm (1.247 mm), width 0.281 to 0.595 mm (0.468 mm). Cuticle not covered by spines or scales. Forebody folded in ventrally, forming scoop shaped pocket, flaring anteriorly, coming together just posterior to the acetabulum. Oral sucker subterminal, circular, 71.9 to 156.9 in diameter. Acetabulum circular, sessile, 93.9 to 196.2, slightly wider than long. Pharynx unmodified, 45.3 to 130.8 long by 42.1 to 137.3 wide. Intestinal bifurcation midway between suckers. Cecae end blindly near posterior of body. Genital pore median, just anterior to acetabulum. Testes tandem, intercecal, wider than long. Anterior testes 48.6 to 340.0 wide by 48.6 to 294.3 long. Posterior testes 48.6 to 340.0 wide by 48.6 to 300.6 long. Cirrus and cirrus sac lacking. Seminal vesicle oval, median, extending to just posterior to acetabulum, narrowing to a tubular pars prostitica with well developed prostate gland.

Ovary circular, 22.7 to 163.5 in diameter, anterior to the anterior testis and dextral of midline. Uterus pretesticular, mostly to left of ovary, emptying into genital sinus. Eggs large, 64.8 to 100.44 by 48.6 to 81.0. Seminal receptacle round, median, in pretesticular space, dorsal to, and slightly overlapping ovary and anterior testis. Vitelline follicles large, extending from posterior edge of acetabulum to posterior of body, confluent posterior to testes.

*Type host.*—Barred Sand Bass, *Paralabrax nubilifer* (Girard).

*Location.*—Intestine.

*Locality.*—Long Beach harbor, Long Beach, California.

*Holotype.*—USNM Helm. Coll. No. 82770.

*Etymology.*—This species is named in honor of Dr. Mike Moser, University of California, Santa Cruz, for his many contributions to marine parasitology.

*Remarks.*—The new species is distinct from *C. caulolotili* Manter, 1940, the only other species in this genus, by its smaller body size (0.601–2.052 mm) versus 2.5–3.3 mm for *C. caulolotili*, lack of tegumental spines and shape of ovary (round of *C. moseri* sp. n. and lobed for *C. caulolotili*).

##### *Proctoeces magnorus* Manter, 1940

(Fig. 2)

Redescription based on 6 specimens. Body aspinose, cylindrical, equally wide along most of length, 1.456 to 4.882 mm (3.356 mm) long by 0.297 to 0.446 mm (0.350 mm) wide. Oral sucker subterminal, muscular, funnel shaped, 327 to 523

Table 1. New host-parasite records for southern California fishes.

Family	Genus 'species	USNM Helm. Coll. #	Host
Digenea			
Acanthocolpidae	<i>Stephanostomum casum</i>	82779	California halibut ( <i>Paralichthyes californicus</i> )
Allocreadidae	<i>Genitocotyle acirrus</i>	82780	White croaker ( <i>Genyonemus lineatus</i> )
	<i>Helicometrina nimia</i>	82773	Starry rockfish ( <i>Sebastes constellatus</i> )
Apocreadidae	<i>Choanodera moseri</i> sp. nov.	82770	Barred sand bass ( <i>Paralabrax nebulifer</i> ) Ocean whitefish ( <i>Caulolatilus princeps</i> )
Fellostomidae	<i>Proctoeces magnorus</i>	82778	California sheephead ( <i>Semicossyphus pulcher</i> )
Gorgoderidae	<i>Probolitrema californiense</i>	82777	Thornback ray ( <i>Platyrrhinoides triseriata</i> )
Hemiuridae	<i>Parahemiurus merus</i>	82772	Deepbody anchovy ( <i>Anchoa compressa</i> )
Opecoelidae	<i>Opecoelus lotellae</i>	82774	California sheephead ( <i>Semicossyphus pulcher</i> ) Scorpion fish ( <i>Scorpena guttata</i> )
	<i>Opecoelina scorpaenae</i> *	82775	Garibaldi ( <i>Hypsypops rubicundus</i> ) White croaker ( <i>Genyonemus lineatus</i> )
	<i>Opecoelina scorpaenae</i> *	82776	California sheephead ( <i>Semicossyphus pulcher</i> )
Monogenea			
Microcotylidae	<i>Microcotyle sebastes</i>	82771	Green rockfish ( <i>Sebastes rastrellager</i> ) Pile surf perch ( <i>Paralichthys vacca</i> ) Shortspine thornyhead ( <i>Sebastolobus alascanus</i> ) Speckled rockfish ( <i>Sebastes ovalis</i> ) Starry rockfish ( <i>Sebastes constellatus</i> )
Nematoda			
Camallanidae	<i>Spirocamallanus perei</i>	82781	Round herring ( <i>Etrumeus acuminatus</i> ) Speckled fin midshipman ( <i>Porichthys myriastes</i> ) Queenfish ( <i>Seriphus politus</i> ) White croaker ( <i>Genyonemus lineatus</i> )
	<i>Spirocamallanus perei</i> (larvae)		Topsmelt ( <i>Atherinops affinis</i> )

\* New locality record.

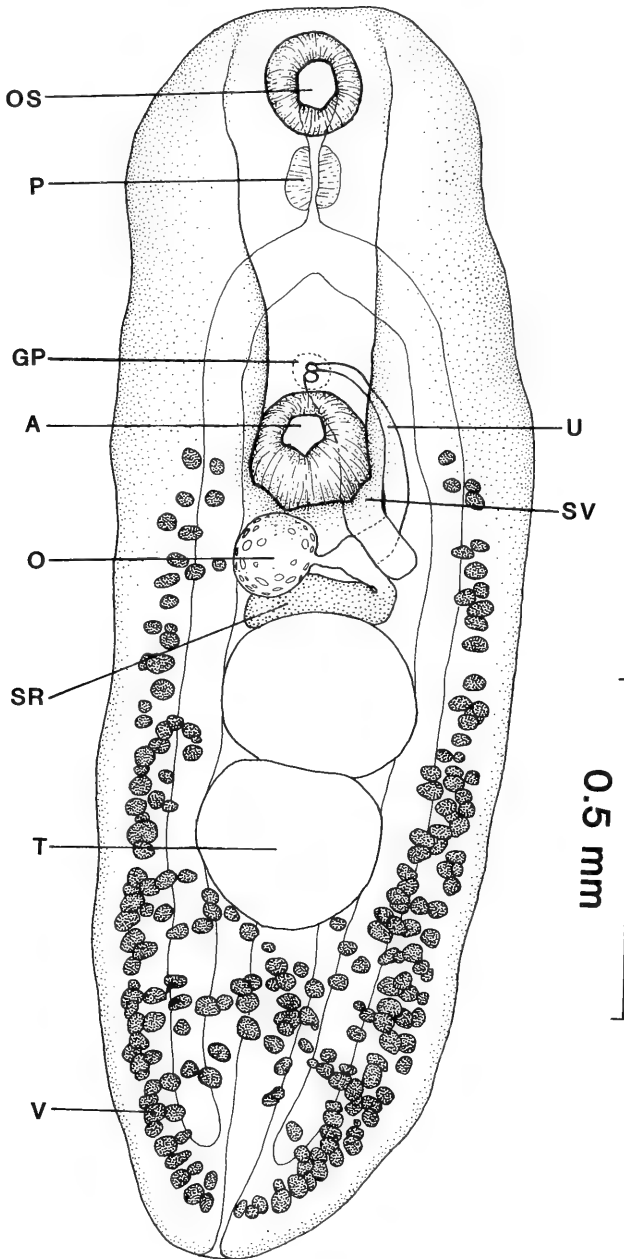


Fig. 1. Line drawing of *Choandera moseri* from composite of immature and mature specimens. A, acetabulum; GP, genital pore; O, ovary; OS, oral sucker; P, pharynx; SR; seminal receptacle; SV, seminal vesicle; T, testis; U, uterus; V, vitellaria.

deep by 359 to 497 wide. Acetabulum pedunculate, 255 to 359 long by 261 to 327 wide, with muscular groove within cavity (not apparent in all specimens). Prepharynx short; pharynx large, very muscular, 233 to 366 long by 117 to 281 wide. Cecae conspicuous, reaching posterior end of body. Intestinal bifurcation

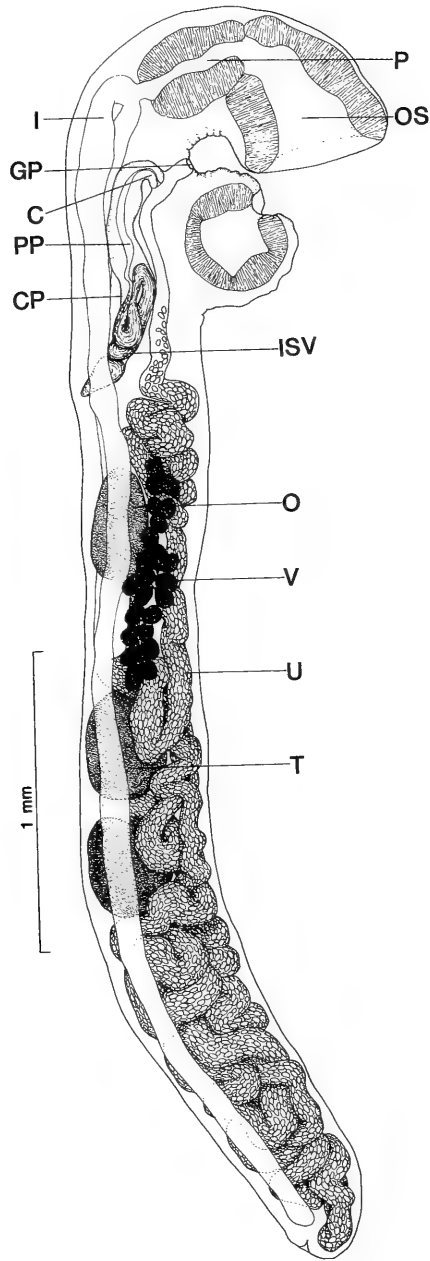


Fig. 2. Line drawing of mature *Proctoeces magnorus*. C, cirrus; CP, cirrus pouch; I, intestine; ISV, internal seminal vesicle; GP, genital pore; O, ovary; OS, oral sucker; P, pharynx; PP, pars prostitica; T, testis; U, uterus; V, vitellaria.

just posterior to pharynx. Genital pore median, anterior to acetabulum stalk, posterior to intestinal bifurcation. Testes oval, diagonal, separated by a few folds of uterus, in posterior half of body, 155 to 385 long by 119 to 281 wide. Cirrus sac claviform, extending to half way between ovary and acetabulum in relaxed

specimens, just posterior to acetabulum in contracted specimens, 392 to 810 long by 65 to 98 wide at greatest width (near base). Posterior portion of seminal vesicle sac like, separated from anterior coiled tubular portion by a constriction. Pars prostitica long, cirrus short, empties into anterior part of a large genital atrium. Ovary oval, pretesticular, 61 to 379 long by 64 to 255 wide, separated from anterior testes by a few coils of uterus. Seminal receptacle seen only in small immature worms, at level of, or slightly posterior to ovary. Uterus extends to and fills posterior portion of body, empties into genital atrium. Eggs small, 19 by 35. Vitelline follicles few, in two lateral groups extending from anterior edge of ovary to anterior testis.

*Host.* — California Sheephead, *Semicossyphus pulcher* (Ayres).

*Location.* — Intestine.

*Locality.* — Long Beach harbor, Long Beach, California.

*Voucher specimen.* — USNM Helm. Coll. No. 82778.

*Remarks.* — Freeman and Llewellyn (1958) synonymized *P. eurythreus* Odhner, 1911 with *P. subtenuis* (Linton, 1907) Hanson, 1950 and concluded that *P. magnorus* was a synonym of *P. subtenuis* (=syn. *P. eurythreus*). Gibson and Bray (1980) placed *P. magnorus* as species inquerendi until more specimens were described. Our specimens compare well with Manter's (1940) original description (USHM #9359), except in three areas: 1. The musculature of the oral sucker is much more distinct in our specimens. 2. The internal seminal vesicle is longer and separated into a sac like posterior section and a coiled tubular anterior portion, and 3. The ovary and testis of our specimens are oval rather than spherical as in Manter's specimen. Since differences within species of *Proctoeces* can be very large (Gibson and Bray 1980; Bray 1983), the variation seen between our specimens and that of Manter, is probably due to variations within the species. Based on this, we concur with Manter (1940) that *P. magnorus* is indeed a distinct species.

#### Discussion

*Opecoelina scorpaenae* Manter, 1934 (Table 1) has not been recorded from any west coast fishes prior to this study (Love and Moser 1983; Gibson and Bray 1984). We found *O. scorpaenae* in three different hosts (Table 1), the California sheephead, *Semicossyphus pulcher* (Ayres), garibaldi, *Hypsypops rubicundus* (Girard), and the white croaker, *Genyonemus lineatus* (Ayres), which suggests that this parasite is common and wide spread.

Sekerak and Arai (1977) reported that specimens of *Stephanostimum casum* (Linton, 1910) found from inshore species of rockfish from the north-eastern Pacific were really *S. californicum* Manter and Van Cleave, 1951 and agreed with Durio and Manter's (1969) assumption that *S. casum* is restricted to tropical waters. *Stephanostimum casum* has been found in fish from the Caribbean, Bermuda, the Mexican Pacific, Galapagos Islands, and the Red Sea (Durio and Manter 1969). Our specimen (Table 1), from the California halibut, *Paralichthys californicus* (Ayres) caught in southern California may represent the northern most extent of *S. casum*'s range.

*Parahemiurus merus* (Linton, 1910) Manter, 1940 is widely distributed in the Gulf of Mexico, Atlantic and Pacific Oceans, as well as Japanese waters, where it is found mostly in carangid, salmonid, clupeid, and engraulid fishes (Bray 1990). *Parahemiurus merus* was reported from 19 species of fish from the western Pacific

Ocean (Love and Moser 1983). The deepbody anchovy, *Anchoa compressa* (Girard) is a new host record for this parasite (Table 1). One other host in the family Engraulididae from southern California, the northern anchovy, *Engraulis mordax* (Girard), has also been found to be infected with *P. merus* (Woolcock 1935). Bray (1990) suggested that *P. merus* could play an important role as a biological indicator. Due to the economic and commercial importance of *A. compressa* and *E. mordax*, and its wide spread prevalence, *P. merus* may make an important biological marker for the management of these fisheries. *Parahemiurus merus*, for example, is used as a marker for the migration of masu salmon, *Oncorhynchus masu* in Japan (Awakuru and Nomura 1983) as well as a stock indicator for the Pacific herring, *Clupea harengus pullasi* in central California (Moser and Hsieh 1992).

Another potentially important biological indicator may be the monogene, *Microcotyle sebastes* Goto 1984, since it is found on the gills in a large number of hosts (Love and Moser 1983). Five new hosts were found to be infected with this parasite (Table 1). Two of the hosts, the starry rockfish, *Sebastes constellatus* (Jordan and Gilbert) and the shortspine thornyhead, *Sebastolobus alascanus* Bean are fished commercially in southern California (Eschmeyer et al. 1983). *Microcotyle sebastes* reach very high levels of infection in the bocaccio, *Sebastes paucispinis* Ayres (Jensen et al. 1982) and may present a potential health problem for stocks of rockfish, a very important component of the sport and commercial fishery in southern California (Eschmeyer et al. 1983).

Nobel and King (1959) listed five new host records for the nematode *Spirocamallanus pereirai* Annereaux, 1946 from southern California. Our study includes four new hosts from southern California waters (Table 1); the round herring, *Etrumeus acuminatus* (Dekay), speckledfin midshipman, *Porichthys myriaster* (Hubbs and Schultz), queenfish, *Seriphus politus* (Ayres), and the white croaker, *Genyonemus lineatus*. Third stage larvae of *S. pereirai* were also found in the intestines of topsmelt, *Atherinops affinis* (Ayres) collected in Malibu Lagoon, Malibu, California.

#### Acknowledgments

I would like to thank Carol Lyons for the drawings of *Choanodera moseri* and *Proctoeces magnorus*.

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## On the Identity of Snapping Shrimp Described and Identified by W. N. Lockington, 1878

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*Abstract.*—W. N. Lockington (1878) wrote the first key and guide to the snapping shrimp of North America. Many records came from the eastern Pacific Ocean, from California to Panama. His paper includes 10 species recognizable today, one record that probably includes more than one species under the same name, and reports and descriptions of another six species that are unrecognizable or questionable. The five species described as new by Lockington probably are variants of species that have been described since 1878; if so, Lockington's species names may be available as senior synonyms. The identities of some of these species are likely to remain uncertain because the original descriptions were brief and without illustrations, the types have been lost and the range of variation within most alpheid species is unknown.

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The first attempt to prepare a summary and key to the snapping shrimp (family Alpheidae) of North America was that of W. N. Lockington of the California Academy of Sciences. In 1878, he published "Remarks on some new Alpei, with a synopsis of North American Species," which presented 18 species. Most of these came from the Pacific Ocean, including the Gulf of California. The paper included species described by Lockington as well as others previously described by Say (1818) and Kingsley (1878a). Lockington considered all of the species to belong either to *Alpheus* or *Betaeus*.

In comparing Lockington's account with modern works on alpheid shrimp, one is surprised by the small number of species. The modern reader should remember that extensive collections had yet to be made in much of the United States and Mexico. Like many curators of the time, Lockington relied upon amateur collectors and fishermen to send specimens to him for examination. The majority of the species known in 1878 were either intertidal species or shallow subtidal species that could be collected in holdfasts or rocks cast ashore after storms.

As was customary at the time, Lockington presented brief descriptions of new species without illustrations. New species were compared with known species, with important morphological differences emphasized. The features presented by Lockington (1878) in many cases only allow the modern reader to determine the genus to which the animal belongs. Features such as presence or absence of epipods, shape of the dactyls of the walking legs, and many of the ridges, grooves and spines of the chelae were not included or were described in general terms. Although locations for the species were given, no type locality was designated if



specimens came from more than one collecting site, nor was a particular specimen mentioned in the text as being a holotype.

Lockington's type material was deposited at the California Academy of Sciences. A few duplicate or exchange specimens seem to have been sent to the Smithsonian Institution or European museums, but as yet, no alpheid specimens have been located. In 1906, almost all of the specimens of the Academy as well as much of the building housing them were destroyed by the fire following the major earthquake in San Francisco. (See Bronson 1959 for an account of how a few of the Academy's specimens were rescued.) No invertebrate specimens are known to have been saved; indeed, being preserved in alcohol, the crustaceans probably were among the first specimens to catch fire.

As part of an ongoing attempt to prepare a master species list of carideans of the tropical eastern Pacific Ocean, M. E. Hendrickx (Estacion Mazatlan, Universidad Autonoma de Mexico) and I have been examining historic records of shrimp of the area. Despite the uncertainty of identification of some of the species, the records given by Lockington are useful for comparison of modern and historic distributions of alpheid species. Kim and Abele (1988) considered five of Lockington's species of *Alpheus* to be valid, but noted that three of the supposed species were unreported since Lockington's report. However, most of Lockington's names have been ignored for over 50 years, and, if found to be senior synonyms of other names, could be suppressed (International Commission on Zoological Nomenclature Article 79c, 1985). This paper provides the modern identification, when known, of Lockington's species of 1878 and attempts to identify the species that remain unrecognized.

### Methods

In the account of the species, the name used by Lockington and the page on which it appears is provided, along with the localities as given in the paper of 1878. Localities are given in quotations if they are vague or questionable in the original text. However, Lockington himself was inconsistent in giving localities, giving localities as "Port Escondido, Gulf of California," which can be interpreted either as Port Escondido in the Gulf of California or Port Escondido as well as the rest of the Gulf of California. (Probably the former interpretation is correct.) Species described prior to 1878 and their current taxonomic status and known range are given first. Species described in the paper are discussed later, with clues to their current identification.

Many of Lockington's specimens came from "Port Escondido" on the Gulf of California (now Puerto Escondido, Baja California Sur, Mexico; 25°50'N, 111°19'W). More recent collecting has been carried out there by the University of Southern California. I examined published records of alpheids collected at Puerto Escondido during the trips of the *Velero III* and later expeditions (Wicksten 1983; Kim and Abele 1988), as well as unpublished records in the card catalogue of the Hancock collections at the Natural History Museum of Los Angeles County. The alpheids from these collections have not been completely identified to species and catalogued by station. However, the existing records give some indication of what species might occur there and therefore might be the same as some of Lockington's species.

## Alpheid Species Reported by Lockington (1878)

## 1. Species Described Prior to 1878:

*Alpheus affinis* Kingsley, 1878a: Panama (p. 476).

Status: Now *Alpheus normanni* Kingsley, 1878b. (*Alpheus affinis* Kingsley, 1878a is a homonym of *A. affinis* Guise, 1854; see Kim and Abele 1988.) Western Atlantic Ocean from Virginia to São Paulo, Brazil and eastern Pacific Ocean from Gulf of California to Galapagos Islands (Kim and Abele 1988).

*Alpheus bellimanus* Lockington, 1877a: San Diego (California) (p. 470).

Status: Valid species; Monterey Bay, California to Galapagos Islands (Wicksten 1983; Kim and Abele 1988).

*Alpheus clamator* Lockington, 1877b: Santa Barbara "Islands," California and San Bartolme Bay, Baja California (p. 469).

Status: Valid species; Dark Gulch, Mendocino County, California (T. Chess, U.S. National Marine Fisheries, personal communication, range extension) to San Bartholome Bay, Baja California Sur (Wicksten 1984).

*Alpheus cylindricus* Kingsley, 1878a: Pearl Island, Bay of Panama (p. 478).

Status: Valid species; eastern and western Atlantic Ocean from Islands of Principe, São Tome and Annobon; Bimini, Bahamas, Bermudas and Florida through Barbados to Bahia, Brazil; Flower Gardens Reefs off Texas; eastern Pacific Ocean from Gulf of California to Galapagos Islands (Kim and Abele 1988).

*Alpheus aequidactylus* Lockington, 1877b: Monterey, California (p. 472).

Status: Now *Alpheopsis equidactylus*; Monterey Bay to Cortez Bank, California (Wicksten 1984).

*Alpheus floridanus* Kingsley, 1878a: Fort Jefferson, Florida (p. 476).

Status: Valid species; eastern and western Atlantic Ocean from Guinea to Congo and Principe Island; Gulf of Mexico to Bahia, Brazil; eastern Pacific Ocean from Gulf of California to Ecuador (Kim and Abele 1988).

*Alpheus heterochaelis* Say, 1818: La Paz, San José Island, Amortiguado Bay, Mulege Bay and Port Escondido, west side of Gulf of California; Magdalena Bay, Baja California (p. 475).

Status: Although *A. heterochaelis* is a valid species, it is considered to inhabit only the western Atlantic (Christoffersen 1984).

Remarks: Kim and Abele (1988) reported that records of *A. heterochaelis* from the eastern Pacific Ocean by Kingsley (1878a) and Rathbun (1900) included in part *A. bouvieri* A. Milne Edwards, 1878. However, it is unclear how they came to this identification, for they did not indicate that they examined the specimens on which the records of *A. heterochaelis* were based. Lockington's specimens may have included *A. californiensis* Holmes, 1900 which has been collected at Magdalena Bay, and other species of the "Edwardsi" group of *Alpheus*, which resemble *A. heterochaelis*. Lockington noted that his larger specimens "showed traces of a varied coloration," which suggests that he had more than one species.

*Alpheus minor* Say, 1818: no locality given by Lockington (p. 472). Say reported it from the "coasts of the southern states, and of East Florida."

Status: Now *Synalpheus minus* (Say, 1818); Bermuda and North Carolina to Alagoas, Brazil (Chace 1972).

*Alpheus panamensis* Kingsley, 1878a: Acajutla, "Central America" (now Pacific coast of El Salvador) and Panama (p. 473).

Status: Valid species; eastern Pacific Ocean from Costa Rica to Peru (Kim and Abele 1988).

*Alpheus parvimanus* Kingsley, 1878a: Panama (p. 477).

Status: Identity unknown.

Remarks: Kingsley's description suggests that the species belonged to the diverse "Edwardsi" group, but, other than mentioning that the larger chela had "a constriction of both margins posterior to the articulation of the dactylus," there are too few details to compare the shrimp with those described more recently.

*Alpheus sulcatus* Kingsley, 1878a: Bay of Panama, Zorritas, Peru (p. 475). Kingsley did not designate a type locality.

Status: Valid species; circumtropical except western Atlantic Ocean, eastern Pacific Ocean from Gulf of California to Peru (Wicksten 1983; Kim and Abele 1988).

*Betaeus aequalis* (Kingsley, 1878a): Catalina Island, California (p. 478).

Status: Synonym of *Betaeus harfordi* (Kingsley, 1878a); Fort Bragg, California to Magdalena Bay, Baja California Sur (Hart 1964).

*Betaeus longidactylus* Lockington, 1877a: San Diego, California (p. 480).

Status: Valid species; Elkhorn Slough, California to Baja California Norte; also northern Gulf of California to Tepoca Bay, Sonora, Mexico (Hart 1964).

## 2. Species Described as New in Paper of 1878:

*Alpheus barbara* Lockington, 1878: Santa Barbara, California (p. 471).

Status: Probably a damaged or malformed specimen of *Alpheus clamator* Lockington, 1877b (Wicksten 1990).

Remarks: Lockington differentiated the supposed new species from *A. clamator* by the absence of a spine on the "basal joint of the antennae" (the basicerite), "different proportions of the carpal joints of the second pair," and the "want of meral spines on the posterior pairs" (of pereopods). However, about 2% of specimens of *A. clamator* lack a spine on at least one basicerite. The "different" proportions of the carpal joints are so close to those of a typical *A. clamator* as to be nearly indistinguishable. Specimens of *A. clamator* usually have a strong spine at the distal end of the merus of the third pereopod, but this could be missing in an animal regenerating a limb. (Kingsley [1878a] and Lockington [1878] both mentioned that the unique holotype of *A. barbara* was "damaged"). Examination of over 1000 specimens collected throughout the range of *A. clamator* failed to locate any animals matching Lockington's description. The type locality of *A. barbara*, Santa Barbara, California, is inhabited by *A. clamator*.

*Alpheus fasciatus* Lockington, 1878: "Port Escondido, Gulf of California" (p. 478).

Status: Kim and Abele (1988) treated *A. fasciatus* as a distinct and valid species "until more information about this species is available."

Remarks: Kim and Abele (1988) believed that *A. fasciatus* was distinct from *A. paracrinitus* Miers, 1881 on the basis of the length of the stylocerite, which, according to Lockington's description, was "longer than the first segment of the peduncle." Otherwise, Lockington's description is almost identical to that of

*A. paracrinitus*. According to Lockington, *A. fasciatus* had "no ocular spines, rostrum about equal to diameter of eye, surface between rostrum and eyes slightly depressed but with no distinct sulcus, small spine on basal joint of antennae below, larger hand smooth, nearly cylindrical, dactylus works vertically, smaller hand small, smooth, cylindrical and slender."

The name "*fasciatus*," meaning banded, gives a clue to the species' modern identity. Lockington described the color as "carapax (sic) and abdomen alternately banded with bright red and white; larger hand red, with marblings of white in some cases." This color pattern is common in *A. paracrinitus*. *Alpheus paracrinitus* has been collected in the southern Gulf of California, where *A. fasciatus* also was reported. *Alpheus paracrinitus* is reported to be circumtropical, in the eastern and western Atlantic Oceans, the Gulf of Mexico, tropical Indo-West Pacific to Hawaii, and eastern Pacific Ocean from the Gulf of California to the Galapagos Islands (Kim and Abele 1988).

Coutière (1897) reported *A. fasciatus* as occurring at Djibouti in the Red Sea. He mentioned seeing specimens of the species from Baja California, collected by Leon Diguët. However, Banner and Banner (1981) noted that the specimens from the Red Sea probably were *A. alpheopsides* Coutière, 1905, which has been collected there recently. Coutière's specimens of *A. fasciatus* have not been located at the Muséum National d'Histoire Naturelle in Paris, but, should they exist, they would be very useful for comparison with other specimens in determining the modern identity of *A. fasciatus*.

Knowlton and Mills (1992) compared color patterns of specimens of *A. paracrinitus* from the Pacific coast of Panama with those of specimens from the Caribbean coast, and found that three different color patterns existed. Specimens from the Caribbean coast showed two discrete patterns that were different from those of the Pacific population. At present, it is not known whether or not these color patterns correspond to separate species or to within-species variation in *A. paracrinitus*. If the color patterns are shown to be related to morphological or enzymatic differences in the shrimp, it may be useful to distinguish the eastern Pacific population by a different species name. Further study may indicate that *A. fasciatus* Lockington is an available senior synonym for the eastern Pacific species.

*Alpheus laeviusculus* Lockington, 1878: Port Escondido, Mulege Bay, and other points on the "Californian" shore of the Gulf of California (p. 474).

Status: Probably a synonym of *Synalpheus digueti* Coutière, 1909.

Remarks: Lockington's choice of the trivial name was poor from the start, for *A. leviusculus* Dana, 1852 is a homonym. However, the description indicates that Lockington's specimen probably belonged to the genus *Synalpheus*. The description states that the front was "trispinose, the ocular spines triangular, almost equal in length to the triangular rostrum, which is not divided from the eye-shields by a rostrum," the chelipeds were "very unequal" in size, and the posterior pereopods had "dactyli bifid at tip, the upper spine longer than the lower."

Coutière (1909) recognized that Lockington's species was a *Synalpheus* and attempted to redescribe and rename it. However, Coutière's new specimens came from off San Nicolas Island in southern California, not the Gulf of California. The new specimens, named *S. lockingtoni*, probably did not belong to

Lockington's original species. In *S. lockingtoni*, the rostrum is longer than the orbital spines, not almost equal to their length. The upper spine of the basicerite is shorter than the lower, but is noticeable; Lockington described this spine as "small" for his species. In *S. lockingtoni*, the stylocerite is shorter than the first segment of the antennular peduncle; in Lockington's species, the stylocerite was described as reaching the middle of the second segment of the antennular peduncle.

Lockington's description could belong to *Synalpheus digueti* Coutière, 1909. In the species, the rostrum is the same length as the orbital spines. The scaphocerite does not reach to the end to the antennular peduncle, the merus of the larger cheliped bears a small spine, and the fingers of the chelae bear dark tips. These features, mentioned by Lockington, occur in specimens of *S. digueti*. *Synalpheus digueti* is a common intertidal species of the southern Gulf of California, and has been collected at Puerto Escondido (Jens Knudsen station K121, collections of Allan Hancock Foundation). It ranges from Guaymas, Gulf of California to the Galapagos Islands (Wicksten 1983).

*Alpheus spinicaudatus* Lockington, 1878: Port Escondido (p. 477).

Status: Kim and Abele (1988) considered *A. spinicaudatus* to be a valid species.

Remarks: Kim and Abele (1988) considered *A. spinicaudatus* to be a distinct species on the basis of the movable finger of the major chela moving obliquely. However, Lockington's description otherwise resembles that of *A. hebes* Kim and Abele, 1988 or a related species of the "Edwardsi" group. The rostrum is described by Lockington as "very short, continued backward between the eyeshields as a low carina, no ocular spine." According to the description by Lockington, the stylocerite was as long as the first segment of the antennular peduncle, the spine of the scaphocerite was longer than the blade or antennular peduncle. The major chela lacked a spine on the merus, the hand bore "constrictions" on the upper and lower surfaces and a sulcus running "backward" longitudinally at right angles to the upper constriction. The smaller chela was rounded and smooth, with the fingertips sharp and curved inwards, crossing each other. The carpus of the second pereopod had 5 articles, the merus of the third to fifth pereopods lacked a spine, the telson was elongate with tapering sides and 2 pairs spinules on the upper surface as well as a pair of posterior spines.

*Alpheus hebes*, which most closely resembles the description of *A. spinicaudatus*, has a short rostrum and no noticeable eyeshields. It ranges from Ensenada de San Francisco, Sonora, Gulf of California to the Galapagos Islands, and has been collected at Puerto Escondido (*Velero III* sta. 670-37) (Kim and Abele 1988). Although *A. hebes* is described as having the movable finger of the major chela closing vertically, Banner and Banner (1982, fig. 83) showed that the shape and angle of the finger varied in *A. edwardsi* within the species. Whether or not similar variation occurs in *A. hebes* is unknown.

*Alpheus tenuimanus* Lockington, 1878: Port Escondido, Gulf of California (p. 473).

Status: Coutière (1899) tentatively identified this as a species of *Synalpheus*.

Remarks: Lockington described this species as "arched in profile, much higher in the centre (sic)." The front was "trispinose, rostrum much longer than ocular

spines, reaching middle of second joint of peduncle of antennulae," the ocular spines were "slender, projecting from the centre of the convex front of the eyeshields." The stylocerite reached beyond the first segment of the antennular peduncle, the basicerite bore a spine and the scaphocerite reached the end of the antennular peduncle. The first pereopods bore a spine at the distal end of the merus. The major chela was elongated and smooth, rounded above and below, with a shallow sulcus and a shorter one "above" extending obliquely upward from the carpal articulation on the inner side of the hand. The smaller chela had a similar merus and an elongated, smooth, cylindrical chela. The second pereopod had a 5-jointed carpus, the third to fifth pereopods were without spines or spinules. The telson was elongate, slightly tapering, with 2 pairs of spinules on the dorsal surface and a spine on each posterolateral border.

Lockington's mention of the "hands" (of the chelipeds) "equal in length, not greatly differing size, dissimilar" casts some doubt on the identification of *A. tenuimanus* as a species of *Synalpheus*, for in the latter genus, the hands differ greatly in size. In species of the eastern Pacific Ocean, it is easy to distinguish between a major and a minor chela; the major chela is not "elongated." The ocular spines were described as "projecting from the centre of the convex front of the eyeshields," rather than "triangular," which suggests that the species belonged to *Alpheus*, not *Synalpheus*.

Two other "trispinose" genera of alpheids occur in the Gulf of California: *Alpheopsis* and *Salmoneus*. However, Lockington himself commented on the "triangular projection on each side of the base of the telson" in the description of *A. aequidactylus* and yet made no mention of such a feature in the description of *Alpheus tenuimanus*. Species of *Salmoneus* have peculiar chelipeds and a very broad rostrum, easily distinguished from that of species of *Alpheus*. It seems most likely that *A. tenuimanus* was a species of *Alpheus*.

Most of the description of *A. tenuimanus* suggests a species of the "Sulcatus" group. Of the species known in the eastern Pacific Ocean, *A. panamensis* Kingsley, *A. felgenhaueri* Kim and Abele and *A. splendidus* Coutière are the most similar. All have a rostrum at least as long as the first segment of the antennular peduncle; the major chela neither has spinules on the merus or characteristic spines, notches or bumps, and there are no large sulci adjacent to the rostrum. However, Lockington stated that the posterior pairs (of pereopods) were "without spines or spinules on any of the joints."

*Alpheus exilis* Kim and Abele, 1988, described from specimens without chelipeds, may be found to be a synonym of *A. tenuimanus*. Both descriptions mention the ocular spines; in both, the third pereopod lacks spines and spinules. However, the rostrum and stylocerite are reported to be shorter than the first segment of the antennular peduncle in *A. exilis*. Length of the rostrum, however, has been found to be variable in at least two species of *Alpheus* (Banner and Banner 1982, figs. 20, 43). *Alpheus exilis* has been taken at Puerto Escondido (*Velero III* sta. 667-37) and Sullivan Bay, Galapagos Islands (Kim and Abele 1988). One hopes that, in the future, a series of specimens with chelipeds can be collected and compared with both descriptions to determine whether or not there are one or two species agreeing substantially with the two descriptions.

## Discussion

Unless Lockington's original specimens are found, identification of many of his species is likely to remain uncertain. Even if some of his specimens are located, identification of the species may remain questionable because, even today, the range of morphological variation within a single species of alpheid shrimp is likely to be unknown. Banner and Banner (1982), in a lengthy study of species of *Alpheus*, contrasted the great variation in features such as length of the rostrum and details of the movable finger of the major chela in various species, while other features remained uniform over a range of the entire Indo-Pacific region. Features such as length of the rostrum and shape of the dactyls of the pereopods in at least two species were found to vary with age and maturity of the animal. Kim and Abele (1988) used features such as rows of setae, spinules of the chelipeds, shape of the ridges and grooves of the major chela and relative lengths of the stylocerite, rostrum and segments of the first antenna to distinguish between species. To date, no one has compared these features among large series of hundreds of animals along the entire eastern Pacific coast. Color patterns of most species are unknown. Some species are known from less than 10 specimens. The dispersal capabilities of eastern Pacific alpheid larvae also are unknown.

In instances in which Lockington's species can be recognized, the species occur today in the localities from which he had specimens. The unidentifiable or questionable species at least are similar to species that still occur in the areas from which Lockington's material came. Lockington's records indicate that at least a few alpheids have occupied the same areas for over 115 years.

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***Amphisamytha fauchaldi*: A New Species of Ampharetid  
(Annelida: Polychaeta) from the  
Hydrothermal Vents at Guaymas Basin, Mexico**

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**Abstract.**—A new species of the polychaete family Ampharetidae, *Amphisamytha fauchaldi*, is described from the hydrothermal vents at Guaymas Basin in the Gulf of California, Mexico, at a depth of 2020 m. This is a very common species in the sampling site. The environment is also described and comments are given about the species inhabiting the area.

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The hydrothermal vents have been studied intensely since they were discovered in 1977 (Corliss et al. 1979). They constitute a most unusual habitat where tectonic activity and toxic emissions (mostly H<sub>2</sub>S) at high temperatures (270–400°C) combine to harbor an exotic and dense fauna (Tunnicliffe 1992).

At Guaymas Basin, the hydrothermal vents differ from others known in the East Pacific Rise, in that there are sediments entering the Gulf of California from the Colorado River. Sediments accumulating at a rate of more than 1 m/1000 years, have covered the rift floor to a depth up to 400 m. Hydrocarbons are formed and percolate through the area (Simoneit 1985). Dense accumulations of organisms, dominated by the giant tubeworm *Riftia pachyptila* Jones, occur in close relationship with the hot springs.

Among the abundant biological material obtained from the *Riftia* washings collected during the Guaymas Basin expedition of February 1988, an undescribed ampharetid was found in large numbers.

The holotype is deposited in the collection of the National Museum of Natural History, Smithsonian Institution (USNM). Paratypes and representatives of the species described were deposited in the collections of the Australian Museum (AM), the British Museum (Natural History) (BM), the Hamburg Zoologische Museum (HMZ), The National Museum of Wales (NMW), the Zoological Museum at the University of Copenhagen (ZMUC), the Muséum National d'Histoire Naturelle de Paris (MNHN), the Los Angeles County Natural History Museum (LANHM), and the Instituto de Ciencias del Mar y Limnología, UNAM, collection (ICML-UNAM), as well as the Dr. J. Frederick Grassle (FG) collection.

#### Study Area

Guaymas Basin is located in the Central region of the Gulf of California, Mexico, approximately at 27°00' North latitude and 111°25' West longitude. The sampling site is located in the Southern Basin in 2000–2020 m depths.

The site was discovered in 1980 (Lonsdale et al. 1982), and has been studied since 1982 (Lonsdale 1984; Grassle 1986). Previous geophysical studies have

shown that in the Gulf of California two large spreading centers exist: the Northern and the Southern Basins.

The Guaymas Basin differs from other hydrothermal active sites in the Pacific Rise in the particular geographic and geological conditions of its spreading centers. Because of land erosion and sediments from the Colorado River and planktonic blooms, there is an organic rich sediment deposit over the area about 400 m deep which prevents therefore lava eruption. One of the consequences of the transport of hot fluids through the organically enriched sediments is the geologically rapid formation of hydrocarbons which percolate through the area (Lonsdale et al. 1980; Simoneit and Lonsdale 1982; Lonsdale 1984).

In the Southern Basin where the samples were taken, the vertical temperature gradients around the bottom are greater than 4°C/m. The sulphur rich fluids that discharge through the chimneys do so at temperatures ranging from 270–314°C.

The site of collection was on the side of a seamount and from soft sediments away from other visible megafauna.

Dense thickets of *Riftia pachyptila* dominate the biota at the seamount. They are often lined with abundant mucus which provides an adequate habitat for a large array of organisms, among them *A. fauchaldi*, a polynoid polychaete and limpets. In addition, there are large mats of light orange and yellowish bacteria known as *Beggiatoa*, several galatheid crabs and some clams. The clams found around the area are small and do not dominate as in other hydrothermal vents.

#### Materials and Methods

The specimens were collected by one of the authors (VSW) in February 1988 using DSRV "ALVIN" Dive 1979, during the Guaymas Basin expedition of 1988 to the Gulf of California. Collections included *Riftia* washings. The specimens were washed and sieved through a 0.3 mm mesh, then fixed in buffered formalin and later preserved in 70% alcohol (Fauchald 1977).

#### Results

##### *Amphisamytha fauchaldi* new species

##### Figures 1A–E

*Material examined.*—Guaymas Basin, Southern Trough, *Riftia* washings, *Alvin* Dive 1979, 18 Feb 1988, 2014 m, holotype (USNM) and 124 paratypes (USNM holotype 168087 + 20 paratypes 168088); AM 10 paratypes (W21709), BM 15 paratypes (1993:5–14); HMZ 10 paratypes (P21986); NMW 10 paratypes (NMW.Z.1993.027); ZMUC 5 paratypes (POL-00020); MNHN 5 paratypes (UD 240 (vial A 923)); LANHM 10 paratypes (LACM-AHF1655); ICML-UNAM 29 paratypes (PO-68-002); and FG 10 paratypes (no numbers assigned).

*Description.*—The holotype is a complete specimen measuring 20 mm long. The paratypes vary from 3.5 mm to 20.5 mm, the most abundant size class being 13.5–14 and 15–16 mm. The smallest ovigerous females are 9.5 mm in length. In Table 1, some morphometric measurements are given from 22 specimens chosen among the total (which was too high to be convenient to include here) so as to give an idea of the variability of the characters present in the different size classes of the mature specimens. Color in life as well as in preserved specimens is light brown. The deep-red heartbody could be seen dorsally over the first seven segments through the translucent body wall in living material.

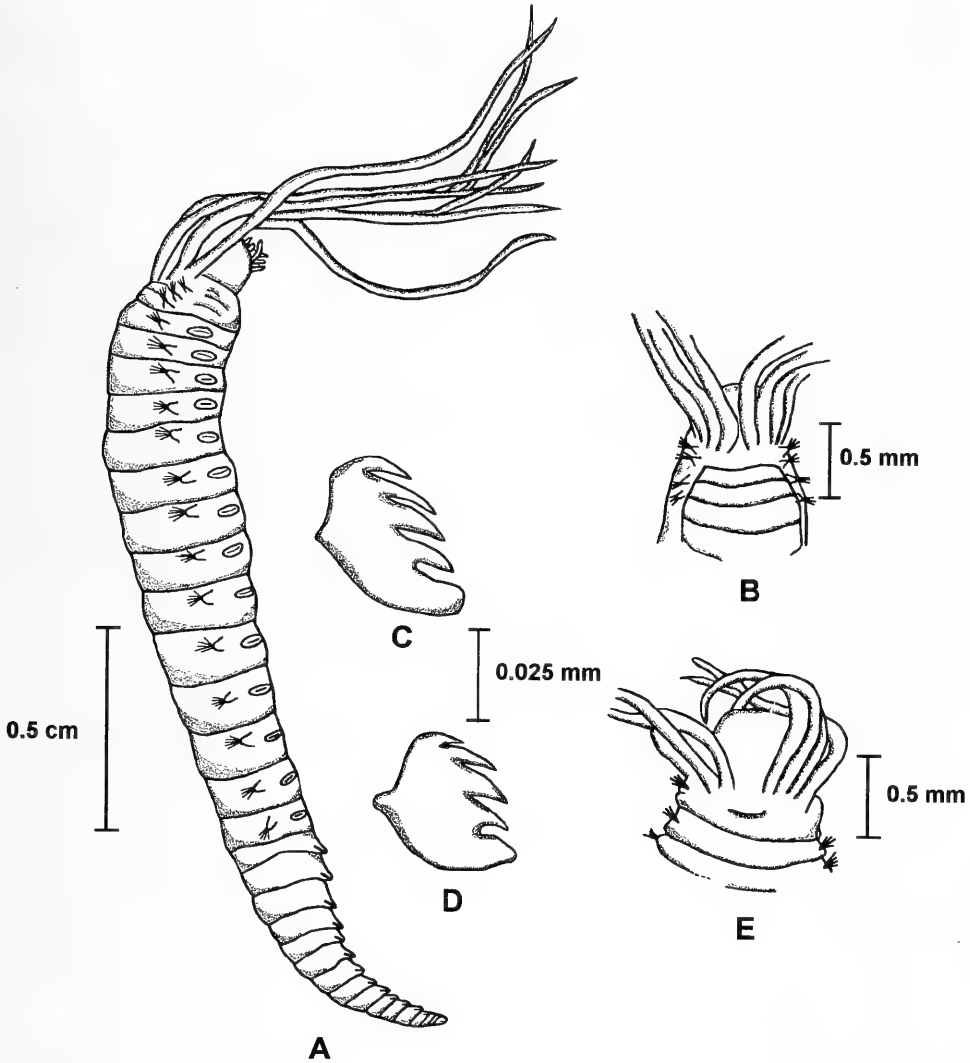


Fig. 1. 1A. *A. fauchaldi*, holotype; entire worm, dorsolateral view. 1B. *A. fauchaldi*, holotype; dorsal view of the prostomium with branchial disposition. 1C. *A. fauchaldi*, holotype; thoracic uncinus. 1D. *A. fauchaldi*, holotype; abdominal uncinus. 1E. *A. galapagensis*, holotype; dorsal view of prostomium with branchial disposition.

The eggs found in the gravid females are small, subcircular with a white central vesicle about one third of the length of an entire brownish egg.

There are 17 thoracic setigers (14 uncinigers) and 13 to 15 abdominal uncinigers (14 in the holotype); (Fig. 1A).

Prostomium indistinctly trilobed and slightly notched with no glandular ridges. Mouth bilobed, oral tentacles numerous, deciduous, ventrally grooved and retractile.

Four pairs of finely annulated long branchiae (approximately 15 mm in holotype), narrowly grooved ventrally, individually inserted across the dorsal surface

Table 1. Some morphometric measurements of *A. fauchaldi*.

	Total length (mm)	Length of branchiae (mm)	Torax width (mm)	No. of setae, fir setiger	Maximum no. of setae in thorax	Maximum no. of thoracic uncini	Length abdomen (mm)	No. of abdominal setigers	Maximum no. of abdominal uncini	Eggs present
H	19.0	15.0	3.0	11	15	59	5.5	15	32	no
	20.0	16.0	4.0	11	16	69	6.0	14	38	no
	17.0	13.0	3.5	12	17	54	5.0	13	30	yes
	17.0	13.0	3.5	10	15	62	4.5	13	28	no
	16.0	12.0	3.0	9	15	55	4.5	14	28	no
	15.0	12.0	4.0	12	15	64	3.5	13	28	yes
	16.0	13.0	3.0	11	16	50	4.5	14	28	no
	18.0	17.0	3.5	11	16	68	5.5	15	28	yes
	13.5	10.0	3.0	10	14	47	3.5	14	24	no
	13.5	10.0	3.5	11	18	58	3.5	14	26	yes
	14.5	9.0	2.5	11	15	55	4.0	14	26	no
	14.0	11.0	3.0	11	16	51	3.5	15	25	yes
	14.5	11.0	3.0	11	16	53	4.5	15	25	yes
	14.0	14.0	3.5	11	16	50	5.0	14	22	yes
	13.5	10.0	3.0	11	16	52	3.0	14	24	no
	10.0	7.0	1.5	9	15	40	2.5	13	18	no
	10.0	9.0	2.0	9	14	44	2.5	15	22	yes
	9.5	11.0	2.0	11	14	38	2.5	14	22	no
	9.5	10.0	2.0	9	14	49	3.0	14	21	yes
	11.0	11.0	3.0	11	14	48	3.0	14	20	yes
	10.0	9.0	2.0	9	14	50	3.0	14	23	yes
	10.0	6.0	1.5	9	12	39	2.5	14	21	no
$\bar{x}$	13.89	11.59	2.86	10.45	15.14	52.50	3.86	14.05	25.41	
S.D.	3.15	2.81	0.73	0.99	1.25	8.33	1.07	0.64	4.40	

H = holotype;  $\bar{x}$  = mean; S.D. = standard deviation.

of segments 2 to 5 so that the first pair is associated to the last asetigerous segment. The inner pair is associated with the last asetigerous segment. The inner pair is associated with the 5th segment in the normal ampharetid fashion. There is no gap between the branchial groups (Fig. 1B).

Segments 1 and 2 fused, ventrally forming the lower lip which shows two ventrolateral grooves. Segment 3 asetigerous. Paleae absent.

First thoracic setiger reduced with a bundle of 10–12 capillary winged smooth notosetae. Second and third setigers are dorsal to the others.

Notopodial lobes bear 15–18 winged smooth capillary setae in two rows with about 7–8 long setae behind 8 short ones.

Neuropodial lobes (uncinigerous pinnules) each with a single transverse row of uncini from setiger 4 to the end of abdomen. Number of thoracic uncini per setiger varies with length of the organism. It can be as high as 68 in longest specimens and around 38 in small specimens (Table 1). The shape of the thoracic uncini is shown in Fig. 1C. They bear four denticles above a squared-off base with a distinct prow; subrostral tip tiny, uppermost denticle smallest.

Abdomen consisting of 13 to 15 (directly related to size) gradually tapering setigers bearing only neuropodial lobes, distinctly different from thoracic ones, rounded, with a glandular pad covering a few uncini and prolonged dorsally.

Shape of thoracic and abdominal uncini shown in Fig. 1C and 1D. Four denticles present. Number of abdominal uncini per setiger is also a function of length, varying from 18 in the smallest to 38 in the largest organisms (Table 1).

Pygidium rounded, bearing two large lateral papillae, three small dorsal papillae and a smoother ventral pad, but no true anal cirri. Anal aperture terminal.

*Tubes.* — Specimens embedded in clumps of many tubes parallel to each other and held together by a mucous substance. There were as many as 20 tubes in a clump. Outer tubes formed by aggregates of fine sediments and different debris, arranged as transverse white and dark brown areas. Inner part of tubes formed by whitish, translucent, vertically oriented linings. Only part of the anteriorly oriented branchiae protruding from the tubes which are simple or branched. Some specimens were found attached to the outer walls of the *Riftia* tubes to which they adhered by similar mucus.

*Remarks.* — Along with *Amphisamytha fauchaldi*, which was by far the most abundant organism, we collected in the clumps several black limpets (7, one of them very small), 26 specimens of *Ophryotrocha akessoni* Blake, six specimens of *O. platykephale* Blake (Solis-Weiss and Hilbig 1992) and one large alvinellid: *Paralvinella grasslei*.

*Etymology.* — This species is dedicated to Dr. Kristian Fauchald, an outstanding polychaetologist, as a small attempt to acknowledge all the help and friendship provided for so many years.

### Discussion

This species belongs to the group of ampharetids with four rather than three pairs of branchiae. It is easily distinguished from the species *A. japonica* (Hessle) and *A. bioculata* (Moore) as mentioned by Zottoli (1983) by the lack of anal cirri and by the possession of glandular pads in the abdominal segments.

*A. fauchaldi* is closely related to *A. galapagensis* Zottoli, also a vent dweller found in the Galapagos site, from which it differs mainly in that there is a clear

Table 2. List of the Annelid Polychaetes reported from the Guaymas Basin.

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Family Alvinellidae
<i>Paralvinella grasslei</i> Desbruyeres & Laubier, 1982
Family Cossuridae
<i>Cossura</i> sp. 1 Grassle et al., 1985
Family Dorvilleidae
<i>Exallopus jumarsi</i> Blake, 1985***
<i>Ophryotrocha akessoni</i> Blake, 1985
<i>Ophryotrocha platycephale</i> (Blake, 1985)***
Family Euphrosinidae
<i>Euphrosine rosacea</i> Blake, 1985
Family Glyceridae
<i>Glycera profundi</i> Chamberlin, 1919
Family Hesionidae
<i>Nereimyra alvinae</i> Blake, 1985
<i>Orseis grasslei</i> Blake, 1985***
Family Nereididae
<i>Ceratocephale pacifica</i> Hartman, 1960***
<i>Nereis sandersi</i> Blake, 1985
Family Polynoidae
<i>Bathykurila guaymasensis</i> Pettibone, 1989***
<i>Branchinotogluma grasslei</i> Pettibone, 1985b
<i>Branchinotogluma sandersi</i> Pettibone, 1985b
<i>Branchiplicatus cupreus</i> Pettibone, 1985a
<i>Lepidonotopodium williamsae</i> Pettibone, 1984
<i>Lepidonotopodium riftense</i> Pettibone, 1984
<i>Macellicephaloides alvini</i> Pettibone, 1989***
<i>Opisthotrochopodus alvinus</i> Pettibone, 1985b
Family Sigalionidae
<i>Neoleanira racemosa</i> (Fauchald, 1972)
Family Spionidae
<i>Lindaspio dibranchiata</i> Blake & Maciolek, 1992***
<i>Spiophanes</i> sp. 1 Grassle et al., 1985

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\*\*\* Species found so far only in the Guaymas Basin.

branchial gap between the two groups of branchiae in *A. galapagensis* (Fig. 1E); such a gap is absent in *A. fauchaldi*. This is a much larger species than *A. galapagensis*, which measures 3–10 mm in length compared to 14–20 mm in *A. fauchaldi*.

*General remarks about the polychaete fauna of Guaymas Basin.*—So far there have been 22 species of polychaetes found in the Guaymas Basin site (Table 2). From these, 17 were newly described from the area (Desbruyeres and Laubier 1982; Blake 1985; Grasse et al. 1985; Pettibone 1984, 1985a, b, 1989; Blake and Maciolek 1992) and two presumably undescribed (*Cossura* sp. 1 and *Spiophanes* sp. 1) (Grasse et al. 1985). Eight species of polynoids mainly in the genus *Branchinotogluma* Pettibone, and dorvilleids with three species represent the highest species richness for this group. The diversity was low as is normal for these

environments but endemism was high. Seven species are known only from Guaymas. Closer examination of additional material may prove that species formerly assigned to already described ones will turn out to be new as in the case of *A. fauchaldi*. The Gulf of California is already known for its endemism, brought about in great part by its configuration with its relatively small opening to the Pacific Ocean.

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