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Distribution, Abundance, and Size Composition of Echinoids from Basin Slopes off Southern California

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Abstract.—Distribution, abundance, and size composition of echinoids from basin slopes off southern California by Bruce E. Thompson, Gilbert F. Jones, Jimmy D. Laughlin, and David T. Tsukada, *Bull. Southern California Acad. Sci.* 86 #3. Four echinoid species are commonly collected from the basin slopes off southern California, and often are the dominant (abundance and biomass) megabenthic species. *Allocentrotus fragilis* is collected in low densities on the upper slopes (150–480 m) of all basins studied. *Brissopsis pacifica* inhabits all slope areas of the region and is most abundant mid-slope (300–600 m). It increases in abundance from the northern to southern nearshore basin slopes. *Brisaster latifrons* is most abundant on upper slopes of the northern nearshore basins and in contrast to *B. pacifica,* it decreases in abundance to the south. *Spatangus californicus* is only a minor component of upper slope assemblages. Although all four echinoid species co-occur on the slopes, there are differences in their abundances among the basin slopes and over slope depth.

Introduction

The sea floor off southern California is a complex region that includes islands, banks, ridges, basins, and troughs (Fig. 1). Basin slopes (approx. 150 m to basin floor) account for about 63% of the sea floor area off southern California (Emery 1960). The basin slopes of the region have been divided into several slope habitat types reflecting depth and proximity to the mainland. Upper (150–500 m) and lower (500 m to basin floor) slopes habitats occur on the nearshore (basins adjacent to the mainland coast) and offshore basin slopes. These designations are based on differences in sediment grain-size and organic material (Malouta 1978; Edwards 1985), Foraminifera (Douglas et al. 1976), and infaunal assemblages (Fauchald and Jones 1979b).

Three echinoid species, *Allocentrotus fragilis* (Jackson), *Brisaster latifrons* (A. Agassiz), and *Brissopsis pacifica* (A. Agassiz), are commonly collected from the basin slopes off southern California and often are the dominant (numerical and/or biomass) megabenthic invertebrates in their assemblages (Mearns et al. 1978; Thompson et al. 1984). Another species, *Spatangus californicus* Clark, also inhabits slopes, but is much less common.

Despite the predominance of these species on the slopes, very little is known about their distribution and ecology in the region. The purpose of this paper is to describe the distributions and abundances of these four echinoids in the south-

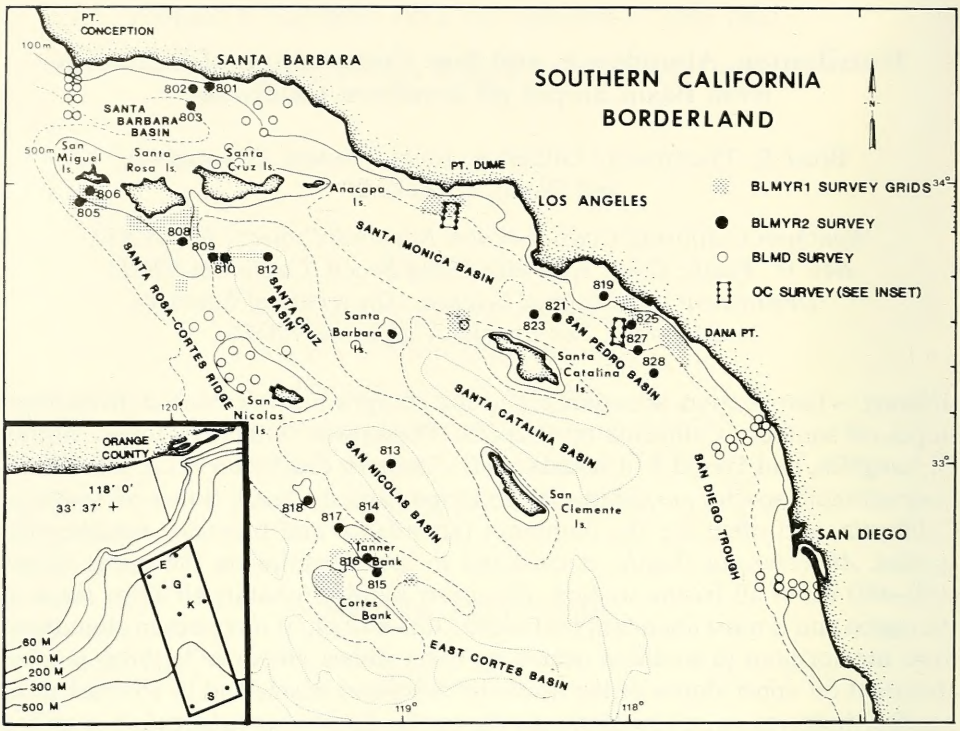

Fig. 1. Sampling locations in the southern California borderland. Inset shows station locations in the San Pedro Basin from the OC survey; an identical station arrangement was sampled in the Santa Monica Basin.

ern California borderland and to provide information on the size composition of their populations on the basin slopes.

Methods

Data were obtained from the following four surveys conducted from 1975 to 1983: the Bureau of Land Management (BLM, now Minerals Management Service) Baseline (hereafter referred to as BLMYR1), Benchmark (BLMYR2), and Descriptive (BLMD) surveys, and surveys conducted on the San Pedro and Santa Monica Basin slopes (supported by Orange County, thus referred to as the OC survey) (see Table 1 and Fig. 1).

The BLM surveys sampled most of the benthic habitats in the region, but each used a different sampling design (Table 1). Box corers are poor samplers of large, motile organisms, but provide the most accurate areal samples for density estimate. The BLM data will be used to describe the distributions and densities of the urchins. Trawling does not provide accurate areal sampling, but provides good distributional and relative abundance information and collects enough specimens for size-frequency analysis; the OC survey trawl data will be used for these analyses.

Analysis of variance (ANOVA, model I) was conducted on the OC survey trawl data using the paired sites at each depth as replicates. Area, depth, year, and

Table 1. Descriptions of the surveys used in this paper. See Fig. 1 for sampling locations.

Survey	Dates	Depths	Survey design	Sampling gear	Reference
BLMYR1	9-75 to 5-76	13–1886	715 single samples from 11, 1 mi^2 grids, plus 45 "scatter" sites.	0.06 m^2 USNEL box corer	Fauchald and Jones, 1983
BLMYR2	1-77 and 8-77	20–1866	8 replicate samples (1000 m radius) from 21 sites in 4 areas.	same as above	Fauchald and Jones, 1979a
BLMD	1-77	13–757	52 single samples from 5 areas; sites arranged in double transects down slope.	same as above	Fauchald and Jones, 1979b
OC	10-81 to 8-83	300–627	8 samples from 2 nearshore basin slopes; sites arranged in double transects downslope.	25′ Otter trawl*	Thompson et al., 1984

* 7.6 m headrope, 4.1 mm mesh net (stretched), 10 min bottom time.

season nested within year were the main effects. The abundances per trawl were transformed by $\log_{10}(n + 1)$ for this analysis since the variances were unequal.

Size-frequency distributions were compiled from test length measurements of 50 urchins collected from trawl samples at each site during each sampling period in the OC survey. Due to the objectives and scope of the OC survey, size-frequency measurements were made only for *A. fragilis* and *B. pacifica.* Total wet weight biomass (kg) of each urchin species and the total invertebrate catch was also measured from the trawls.

Analysis of the size-frequency distributions was conducted using the Kolmogorov-Smirnov test (two samples) and G testing (more than two samples; Sokal and Rohlf 1969). G testing was conducted using both 1- and 5-mm size class intervals and producd the same conclusions (significance, $\alpha = 0.05$). We will present the 1-mm size data as they show the most information.

Results

Allocentrotus fragilis (Jackson)

Distribution and densities.—During the BLMYR1 survey, *A. fragilis* was collected from both nearshore and offshore slope areas (Table 2). Densities up to 2.8 m^{-2} were recorded on the nearshore basin upper slopes, but densities were highest offshore, on the upper slopes of the Santa Cruz Basin, where up to 6.2 m^{-2} were collected.

During the BLMYR2 and BLMD surveys, this species was additionally collected from the slopes of the Santa Barbara Basin. Although none was collected from sites in the San Diego Trough or on the San Nicolas Is. shelf during these surveys

Table 2. Mean densities and frequencies of occurrence of 3 echinoid species from the BLMYR1 survey. *Spatangus californicus* was not collected in any of the box core samples.

Area Habitat	Number of sites	Depths (m)	Mean number m^{-2} (frequency)		
			A. fragilis	*B. pacifica*	*B. latifrons*
San Pedro Basin					
Upper slope	23	161–520	2.0 (.13)	7.0 (.39)	0.7 (.04)
Lower slope	20	532–652	0	4.0 (.20)	0
Santa Monica Basin					
N. upper slope	13	303–632	0	11.1 (.46)	9.8 (.46)
S. upper slope	24	522–744	0	19.8 (.82)	0
N. lower slope	17	222–461	2.8 (.18)	0.7 (.04)	0
S. lower slope	10	480–851	1.6 (.10)	0	0
Santa Barbara Basin					
Upper slope	8	144–203	0	4.0 (.25)	14.0 (.25)
Santa Cruz Basin					
Upper slope	13	129–422	6.2 (.23)	4.9 (.15)	0
Lower slope	20	541–1768	0	2.1 (.13)	0
East Cortes Basin					
Lower slope	19	722–1247	0	1.7 (.11)	0
San Miguel Island					
Shelf-ridge	31	122–500	0.5 (.03)	5.7 (.19)	0.5 (.03)
Santa Rosa Island					
Shelf-ridge	102	26–479	2.2 (.03)	2.5 (.14)	0.3 (.01)
Tanner and Cortes Banks	47	81–345	0.7 (.04)	2.0 (.11)	0.3 (.02)

(Table 3), specimens have been collected from the San Diego Trough slopes in subsequent surveys (SCCWRP unpubl.). As in the BLMYR1 survey, the highest densities were collected from the slopes of the Santa Cruz Basin, up to 6.0 m^{-2} at Sta. 810. Indices of dispersion (Fisher 1970) were not significantly different ($\alpha = 0.05$; 7 df) from random in any of the replicated samples (Table 3), and no significant seasonal (winter–summer, 1977) differences in the densities of *A. fragilis* were found at any of the BLMYR2 sites (Mann-Whitney $U > 12$, $\alpha = 0.05$).

The depth range in the southern California borderland is from 48 m on the San Miguel Is. shelf to 851 m on the lower slopes of the Santa Catalina Basin; however, this species is generally restricted to the outer shelf and upper slope between 100 and 480 m. This species inhabits a wide range of sediment types from fine biogenic sand to very fine silt (mean phi = 2.3–7.8; total organic carbon = TOC = 0.3–2.7%).

Trawl catches.—Otter trawl catches from the OC survey on the slopes of the San Pedro and Santa Monica basins show trends in abundance of *A. fragilis* over slope depth (Fig. 2A). The largest catches (up to 1251 urchins) were from 300 m on the upper slopes in both basins. At these sites *A. fragilis* contributed up to 94% (maximum of 54 wet kg) to the total megabenthic invertebrate biomass.

Significantly more *A. fragilis* were collected at the 300 and 380 m sites than at the 480 m site in both basins ($F = 75.70$, $P = 0.0001$). Although catches were slightly larger in the Santa Monica Basin, there was no significant difference in

Table 3. Mean densities and Fisher's Index of Dispersion (BLMYR2 only) or frequencies of occurrence (BLMD only) for four echinoid species from the BLMYR2 and BLMD surveys. W = winter, S = summer.

Area (survey) Station(s)	Season	Depth (m)	n	Mean number m^{-2} (Chi-square) or [frequency] *A. fragilis*	*B. pacifica*	*B. latifrons*	*S. californicus*
San Diego Trough (BLMD)							
Upper slope	W	180–474	3	0	16.0 [1.0]	0	0
Lower slope	W	652–757	4	0	12.0 [.50]	0	0
San Pedro Basin/San Diego Trough (BLMYR2)							
Lower slope							
827	W	527	8	0	2 (7.0)	0	0
	S			0	2 (7.0)	0	0
828	W	567	8	0	2 (7.0)	0	0
	S			0	2 (7.0)	0	0
San Pedro Basin (BLMYR2)							
Upper slope							
825	W	256	8	0	2 (7.0)	4 (6.0)	0
	S			2 (7.0)	2 (7.0)	0	0
Santa Barbara Basin							
Upper slope							
802 (BLMYR2)	W	337	8	0	0	16 (6.0)	0
	S			0	2 (7.0)	30 (7.9)	0
(BLMD)	W	190–453	8	2 [.13]	2 [.13]	18 [.63]	0
Santa Cruz Basin (BLMYR2)							
Upper slope							
808	W	105	5	3.2 (4.0)	6.4 (3.0)	0	0
	S		8	4 (14.0)	16 (4.0)	0	0
809	W	255	8	0	6 (10.3)	0	0
	S			4 (6.0)	14 (12.4)	0	2 (7.0)
810	W	468	8	6 (10.3)	18 (11.4)	0	2 (7.0)
	S			4 (6.0)	14 (4.5)	2 (7.0)	2 (7.0)
San Miguel and Santa Rosa Is. (BLMYR2)							
Shelf-ridge							
805	W	239	8	2 (7.0)	2 (7.0)	0	0
	S			0	8 (8.0)	2 (7.0)	0
806	W	99	8	0	2 (7.0)	0	0
	S			0	4 (6.0)	0	0
San Nicolas Is. (BLMD)							
Shelf-ridge	W	59–713	11	0	5.8 [.18]	0	0
Tanner Bank (BLMYR2)							
816	S	75	8	2 (7.0)	0	0	2 (7.0)
818	W	179	8	0	42 (30.4)*	0	2 (7.0)

* Chi-square is significant, $\alpha = 0.05$.

catches between the two basin slopes in 1983 ($F = 0.43$, $P = 0.519$). There were significantly larger catches in 1983 than in 1982 on the San Pedro Basin slopes ($F = 6.35$, $P = 0.027$), but no significant difference between the winter and summer catches within each year were shown ($F = 1.99$, $P = 0.179$) for either area.

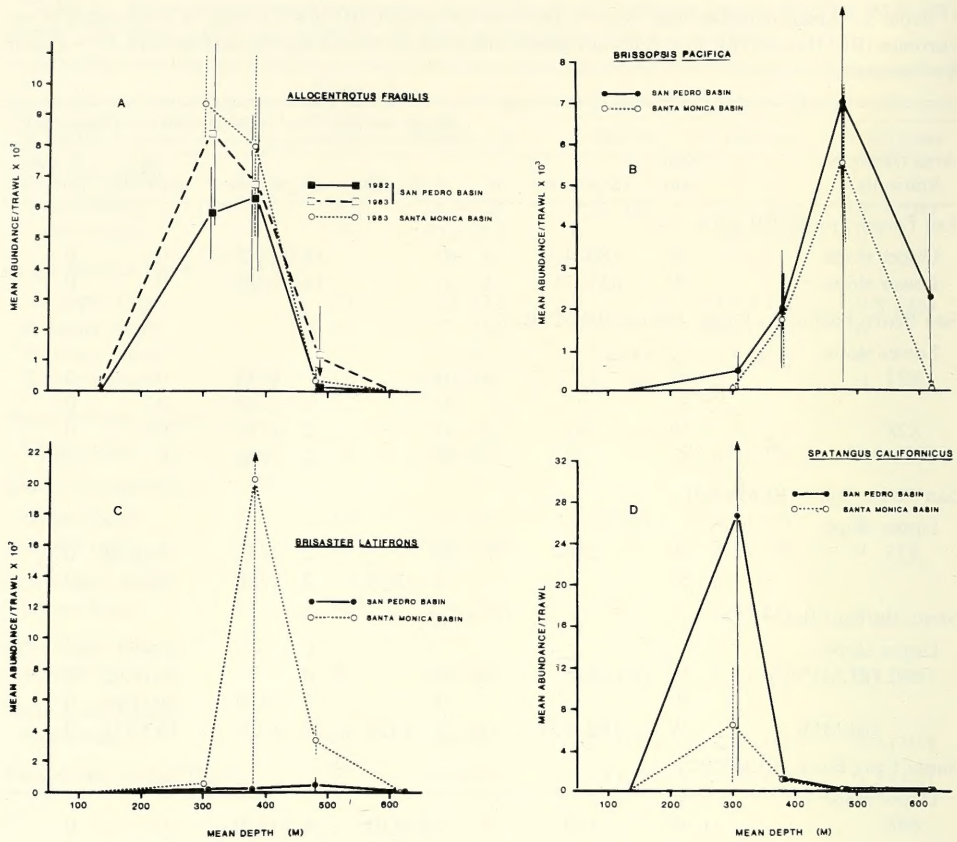

Fig. 2. Mean abundances per trawl (±1 std. dev.) of four echinoid species on two nearshore basin slopes; data from OC survey. All samples from each depth were averaged, N = 8 for San Pedro Basin slopes and N = 4 for the Santa Monica Basin slopes.

Size composition.—Populations on the San Pedro and Santa Monica Basin slopes were composed mostly of adults (larger than 30 mm). Most samples showed polymodal size distributions which suggests multiple age classes (for example, Fig. 3A); however, we cannot preclude the possibility of having trawled through several single cohort patches. Juveniles (smaller than 15 mm) were only collected in one sample during the OC survey (San Pedro Basin Sta. G16, summer, 1983).

Comparisons of size-frequency distributions between pairs of samples collected at the same depths and times (i.e., Fig. 3A) showed that 70% of the pairs were composed of significantly different size distributions (Kolmogorov-Smirnov test, $\alpha = 0.05$). Urchins were significantly larger at the 300 m sites than at the 380 m sites ($G = 87.0$, $df = 39$), and Santa Monica Basin slope urchins were significantly larger than those from the San Pedro Basin slope ($G = 151.3$, $df = 39$; Fig. 3B). Size composition did not change significantly among the three samples collected over time (summer 1982, winter, summer 1983) on the San Pedro slope ($G = 71.2$, $df = 78$), but sizes were significantly larger in winter than in summer, 1983 ($G = 125.7$, $df = 39$) on the Santa Monica Basin slope.

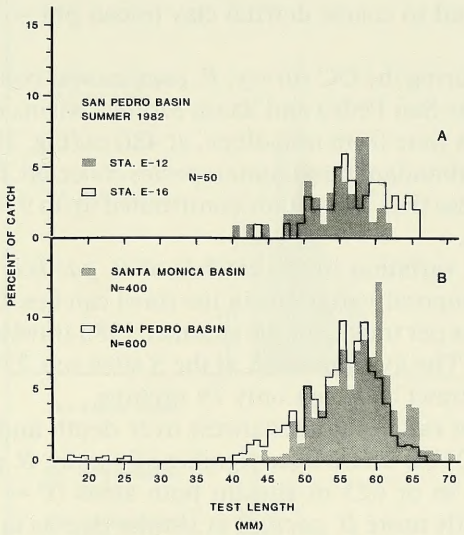

Fig. 3. Average size-frequency distributions of *A. fragilis* populations from two nearshore basin slopes. A. Example of differences in size from two stations at the same depth. B. Difference in sizes between basin slope populations, all samples pooled.

Brissopsis pacifica (A. Agassiz)

Distribution and densities.—During the BLMYR1 survey this species was collected from all of the basin slopes studied (Table 2). Nearshore, densities were highest on the southern upper slopes of the Santa Monica Basin where an average of 19.8 m^{-2} were collected. Offshore, *B. pacifica* densities were generally lower than on the nearshore slopes, ranging from 2.0–5.7 m^{-2} on the insular shelves, ridges, and banks (Table 2); however, samples from 2 "scatter" sites (not shown on Fig. 1) on the upper slopes of the East Cortes Basin had average densities of 24 m^{-2}.

During the BLMYR2 and BLMD surveys *B. pacifica* was additionally collected from the slopes of the San Diego Trough and the San Nicolas Is. shelf (Table 3). Densities were consistently low, reaching only 2 m^{-2} on the nearshore basin slopes. Offshore, densities were higher reaching 18 m^{-2} at Sta. 810 on the upper slopes of the Santa Cruz Basin. At Sta. 818 on Tanner Bank, unidentifiable spatangoids (juveniles and damaged specimens) believed to be *B. pacifica* were collected in average densities of 42 m^{-2}. Except for the Sta. 818 samples, none of the BLMYR2 replicate samples showed indices of dispersion significantly different ($\alpha = 0.05$; 7 df) from random (Table 3), and there were no significant differences in densities between the winter and summer (1977) samples at any BLMYR2 site (Mann-Whitney $U > 12$, $\alpha = 0.05$). Samples from the BLMD survey showed the highest densities on the upper slopes of the San Diego Trough, up to 16 m^{-2} (Table 3).

The depth range of *B. pacifica* in the southern California borderland is between 52 m of the San Miguel Is. shelf, and 1215 m (the deepest record for this species) on the lower slopes of the Santa Cruz Basin. Usually, it is restricted to upper and mid-slope depths. This species inhabits a wide variety of sediment types ranging

from fine biogenic sand to coarse detrital clay (mean phi = 2.4–8.9; TOC = 0.5–4.6%).

Trawl catches.—During the OC survey, *B. pacifica* was collected from the upper and lower slopes of the San Pedro and Santa Monica basins between 300 and 625 m. The largest catches were from mid-slope, at 480 m (Fig. 2B), where this species was usually the most abundant megafaunal species collected. Biomass of *B. pacifica* was also highest at these sites where they contributed up to 97% of the megabenthic invertebrate biomass.

A large amount of variation in the catches of *B. pacifica* is shown in Fig. 2B, and is due to large temporal variations in the trawl catches. Catches at the K sites averaged 6900 urchins per trawl, but the summer 1983 trawl at Sta. K16 contained over 21,000 urchins. The average catch at the S sites was 2200 urchins per trawl, but the winter 1983 trawl collected only 29 urchins.

Differences in trawl catches (abundances) over depth and between areas were compared using ANOVA. There were significantly more *B. pacifica* at the 480 m sites than at the 300 m or 625 m sites in both areas ($F = 25.54$, $P < 0.0001$). There were significantly more *B. pacifica* at similar depths in the San Pedro Basin than in the Santa Monica Basin ($F = 28.79$, $P < 0.0001$). In the Santa Monica Basin, *Brisaster latifrons* was most abundant. There were no significant differences in trawl catches (abundances) between years (1982, 1983) in the San Pedro Basin samples ($F = 2.41$, $P = 0.140$) or between seasons (winter, summer) in either basin ($F = 0.83$, $P = 0.368$).

Size composition.—The populations on both basin slopes were composed mostly of adults (larger than 20 mm). Most samples showed polymodal size distributions which suggests multiple age classes (e.g., Fig. 4A). Juveniles (smaller than 15 mm) were only collected in one sample during the OC survey (San Pedro Basin Sta. G16, winter, 1982).

Comparisons of size-frequency distributions between pairs of samples collected at the same depths and times (i.e., Fig. 4A) showed that 69% of the pairs were composed of significantly different size distributions (Kolmogorov-Smirnov test, $\alpha = 0.05$). Urchins from the San Pedro Basin slopes were significantly larger on the lower slope than on the upper slope ($G = 591.3$, $df = 1$), but no such difference was found on the Santa Monica Basin slopes ($G = 56.8$, $df = 1$; Figs. 4B, C). Santa Monica Basin slope urchins were significantly larger ($G = 264.1$, $df = 39$) than those from the San Pedro Basin slopes at similar depths. Urchins' sizes increased significantly over two years on the San Pedro Basin slopes ($G = 345.8$, $df = 132$).

Brisaster latifrons (A. Agassiz)

Distribution and densities.—In the BLMYR1 survey, *B. latifrons* was collected from most of the areas sampled (Table 2). It was most frequently collected on the upper slopes of the northern nearshore basins. Densities were highest on the upper slopes of the Santa Barbara Basin where up to 14 m^{-2} were collected. Densities decreased from the northern to the southern nearshore basin slopes and decreased over slope depth. Densities on the offshore basin slopes were very low, averaging less than 0.5 m^{-2}.

During the BLMYR2 survey, as in the YR1 survey, densities were highest on the upper slopes of the Santa Barbara Basin, reaching 30 m^{-2} at Sta. 802 (Table

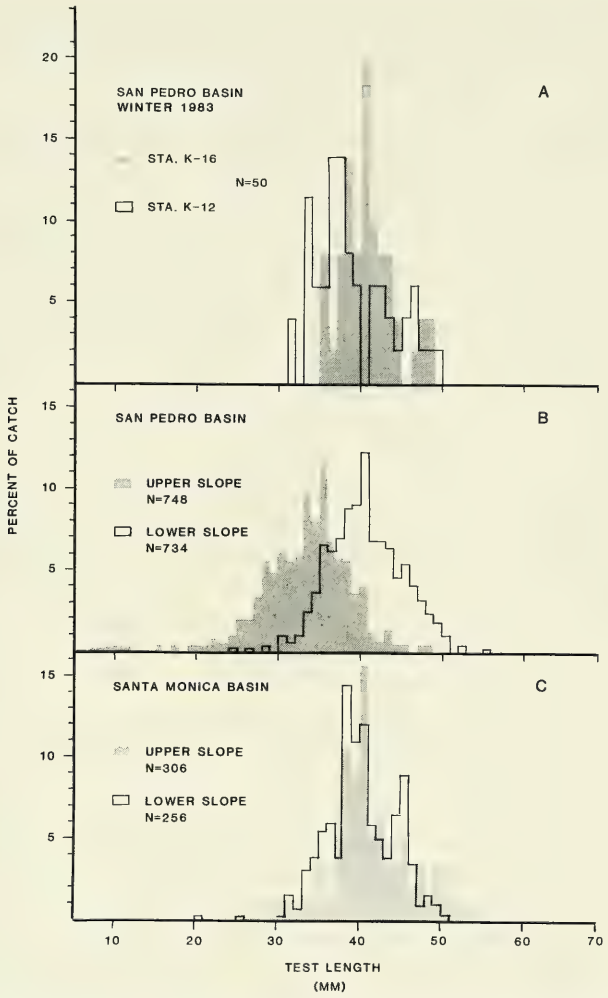

Fig. 4. Average size-frequency distributions for *B. pacifica* populations from two nearshore basin slopes. A. Example of size differences at two stations, same depth. B. Differences between upper and lower slope samples in the San Pedro Basin, all samples pooled. C. Upper and lower slope population sizes on the Santa Monica Basin slopes, all samples pooled.

3). Similarly high densities were found in the BLMD transects in that basin. Only two specimens were collected from the offshore areas during the BLMYR2 survey, for average densities of 2 m^{-2} where collected. Indices of dispersion calculated for the BLMYR2 replicated samples showed no significant differences ($\alpha = 0.05$, 7 df) from random dispersions for any of the samples (Table 3), nor were there any significant seasonal differences (winter, summer 1977) in densities at any of the BLMYR2 sites (Mann-Whitney $U > 12$, $\alpha = 0.05$).

The depth range of *B. latifrons* in southern California is between 85 m off Pt. Dume, to 780 m on the lower slopes of the San Pedro Basin; however, it is usually restricted to the upper slopes (150–500 m). This species inhabits mainly soft, muddy sediments (mean phi = 4.1–7.8; TOC = 0.8–2.7%).

Trawl catches.—Data from the OC survey show the trends in abundance of *B. latifrons* over slope depth and differences in abundance between the San Pedro and Santa Monica Basin slopes (Fig. 3C). In the Santa Monica Basin, it was occasionally the most abundant megabenthic invertebrate collected and it contributed up to 61% to the trawl catch biomass. In the San Pedro Basin it contributed less than 1% to the trawl catches.

The large amount of variation in the trawl catches of *B. latifrons* at the 380 m sites on the Santa Monica Basin slopes was because *Brisaster latifrons* and *Brissopsis pacifica* alternately dominated the winter, 1983 catches at those sites. At Sta. G12, *B. latifrons* contributed 80.9% and *B. pacifica* contributed 12.5% to the trawl catches (abundance). At Sta. G16 (same depth as G12, 2 km away) the relative abundances were nearly opposite: *B. latifrons* contributed 12.8% and *B. pacifica* contributed 62.8% to the catches.

Spatangus californicus H. L. Clark

Distribution and densities.—During the BLMYR1 survey, it was not collected in any box core samples. During the BLMYR2 survey, single specimens were collected from two sites on the Santa Cruz Basin slopes, and two sites on Tanner Bank, for average densities of 2 m^{-2} (Table 3). This species was also collected in trawls from the upper slopes of the Santa Barbara Basin and the San Diego Trough during more recent surveys (SCCWRP unpubl.).

The depth range of *S. californicus* off southern California is from 150 to 380 m on the upper slopes, a much narrower range than the other echinoids. It inhabits a wide variety of sediment types ranging from fine sand to very fine silt (mean phi = 2.3–7.3; TOC = 0.3–2.3%).

Trawl catches.—*S. californicus* was collected in otter trawls during the OC survey from the upper slopes of the San Pedro and Santa Monica basins. This species was most abundant at 300 m on the upper slopes in both basins, but was more abundant on the San Pedro Basin slopes than on the Santa Monica Basin slopes (Fig. 3D). This species contributed an average of 9% to the megabenthic invertebrate biomass on the San Pedro slopes and 3% to the biomass in the Santa Monica slopes. The largest catch of this species was on the San Pedro Basin upper slope at Sta. E16 in June 1982 where 60 urchins were collected. Off southern California, *S. californicus* is the largest of the four species of urchins considered in this paper, growing up to 100 mm in length.

Discussion

The distributions of the four echinoid species considered in this paper overlap in the southern California borderland. They all occur in highest densities on basin slopes and often are collected in the same sample; however, differences in abundances of each species exist among the different basin slopes and over slope depth.

Allocentrotus fragilis occurs in highest densities on the upper slopes of the Santa Cruz Basin. It dominates trawl catches (abundance and biomass) on the upper slopes of the San Pedro and Santa Monica basins and was reported to be the most abundant megafaunal species collected on the San Miguel Is. shelf and Tanner Bank (75–330 m), in a trawl survey conducted by Mearns et al. (1978) as part of the BLMYR2 studies. Densities of *Brissopsis pacifica* are also highest on the offshore slopes. Densities from the BLM surveys were variable, being high (>15

m^{-2}) in different areas in each survey. On the nearshore slopes, densities increase from the northern to southern basins, and it dominates trawl catches from mid-slope in the San Pedro and Santa Monica basins. *Brisaster latifrons* occurs in highest densities on the upper slopes of the Santa Barbara Basin. In contrast to *B. pacifica,* densities decrease from the northern to southern nearshore slopes, and it is rarely collected from the offshore ridge-banks and basin slopes. *Spatangus californicus* has a much more restricted distribution than the other irregular urchins. It inhabits both nearshore and offshore slopes, but is only a minor component of slope megabenthos in the region. It is collected in trawls in low abundances, but has not been collected in grab or core samples from the nearshore basins in any survey, suggesting that individuals are widely spaced.

Peak abundances of each echinoid species occur at a slightly different depth on the nearshore slopes (Fig. 2). Although both *A. fragilis* and *S. californicus* are most abundant at 300 m, the latter is much less abundant and is restricted to a narrower depth range on the upper slopes.

The size composition of *A. fragilis* and *B. pacifica* populations on the nearshore slopes is heterogeneous over slope depth, between slopes, and over time. Populations of both species are composed of several adult size-classes; juveniles of each species were collected only once over two years in the OC study. The largest urchins of both species occur where they are most abundant, and urchins of both species are larger on the Santa Monica Basin slopes than on the San Pedro Basin slopes.

Factors that influence the distribution and abundance patterns described in this paper are not clear. There is no restriction to a particular sediment type. All four species inhabit a range of sediment types from fine biogenic sand (mean phi = 2.3) on the offshore shelves, ridges, and banks to very fine silty clay on the nearshore lower slopes (mean phi = 7.8); organic carbon values range from 0.3 to 4.6%. Maximum abundances may be related more to food availability than to sediment type. *A. fragilis* is most abundant on the offshore slopes, shelves, and banks where infaunal diversity is highest, perhaps a reflection of their predator-scavenger feeding mode. *B. pacifica* occurs in highest densities on the offshore basin lower slopes where sediment organic levels are highest, reflecting their detritivorous feeding mode.

No echinoids have been collected from the basin floors of the region. These areas are within the depth ranges reported for all of the species considered in this paper except *S. californicus.* The absence of echinoids from the basins may be related to the very low dissolved oxygen concentrations (below 0.5 ml l^{-1}) on the basin floors.

The depth distribution and abundances of *A. fragilis* and *B. latifrons* off southern California are similar to those reported off Oregon where they also co-occur. Alton (1972) reported the largest trawl catches of *A. fragilis* from 177–232 m, slightly shallower than our peak catches at 300 m. He also reported considerable variability in the number of urchins per catch and suggested that *A. fragilis* exists in aggregated populations, but we could not demonstrate any such aggregation in our data. Densities averaging 0.5 m^{-2} were reported by McCauley and Carey (1967) from Oregon, slightly lower than the densities we have reported. *A. fragilis* grows to larger sizes off Oregon (up to 92 mm) and central California (up to 103 mm; Boolootian et al. 1959) compared to our largest urchin of 72 mm.

Brisaster latifrons (as *B. townsendii,* see McCauley 1967 for synonymy) occurs over depths of 100–840 m in densities of 3.8–30.0 m^{-2} off Oregon (McCauley and Carey 1967; Alton 1972). In Puget Sound, this species occurs in average densities of 47 m^{-2}, and they are uniformly dispersed. These densities are much higher than those we have reported, and we could show no differences from random dispersion. In Puget Sound, this species grows up to 60 mm in length compared to our maximum size of 73 mm (Lie 1968; Nichols 1975).

Three other echinoid species have also been collected from slope depths in the southern California borderland. The regular urchin *Lytechinus pictus* (Verrill) is usually restricted to shallower shelf depths (15–205 m). It was collected from the ridges, banks, and slopes in the BLM studies where it co-occurred with *A. fragilis, B. latifrons,* and *B. pacifica* at some sites. The irregular urchins *Gonomaritia laevis** (Clark) and *Lovenia cordiformis* (Agassiz) have been collected (once each in the BLMYR2 survey) from the offshore ridge-bank areas, *G. laevis* at Sta. 816 on Tanner Bank, and *L. cordiformis* at Sta. 805 on the San Miguel Is. shelf. Other collections in the region were recorded by Clark (1948).

Of the seven echinoid species that inhabit the southern California basin slopes, only *A. fragilis* and *B. latifrons* range north to Oregon and Washington. In contrast, all seven species have been collected along the Baja peninsula to the south (Grant and Hertlein 1938; Clark 1948).

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Geographic Variation in Vocalizations of California Chipmunks *Tamias obscurus* and *T. merriami*

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Abstract.—Vocalizations of chipmunks were analyzed from isolated mountain ranges of California to determine the extent of interspecific and intraspecific variation in chip calls. For calls recorded, based on five measurements per emission, the two species showed significant differences in vocal parameters measured from sonagrams. Significant intraspecific variation in chip calls suggests that populations of chipmunks have achieved a level of divergence in chip calls in some cases equivalent to differences between populations belonging to different species. The terminal pulse is first described for *Tamias merriami,* along with a presentation of the previously undescribed *T. obscurus* vocalization pattern.

Vocalizations are involved in the communication behavior of most sciurids, including ground squirrels (Harris et al. 1983; Leger et al. 1984), tree squirrels (Viljoen 1983), and marmots (Waring 1966), and are known to be species specific in prairie dogs (Waring 1970). Chip calls have been shown to be species specific in chipmunks (Brand 1976) and are reported to be emitted during courtship (Callahan 1981).

Brand (1976) described the "chip" of California species of *Tamias* and found it to contain consistent interspecific differences, unlike other vocalizations of *Tamias* (such as the chatter, trill, and chuck). This interspecific variability suggests that perhaps the chip could play a rôle in species recognition, individual recognition, and mate selection and therefore was the focus of our investigation.

In this study we describe the chip for *Tamias obscurus* and analyze geographic variation in this call. The calls of *Tamias obscurus* are compared with those of sympatric and allopatric populations of *Tamias merriami.* The diagnosis of *Tamias obscurus* by Callahan (1977) is based on morphological characters and does not include a vocal description.

Study Areas

Calls were recorded from four California study sites (Fig. 1) chosen for a comparison of allopatric and sympatric divergence of calls. Two were in the San Bernardino Mountains (SBD), in San Bernardino County: five Km north of Onyx Summit (*Tamias obscurus*) and 1.6 Km northeast of Green Valley Lake (*T. merriami*). The third (both *Tamias obscurus* and *T. merriami*) was in the San Jacinto Mountains (SJ) on the slopes of Black Mountain, in Riverside County, and was isolated from the first two sites by a broad strip of semi-desert habitat. The fourth study site (*T. merriami*) was located at Columbia (Col) in Tuolumne County.

Fig. 1. Map of the distribution of *Tamias obscurus* (stippled) and *Tamias merriami* (cross-hatch) with the study sites identified. Based on Hall (1981).

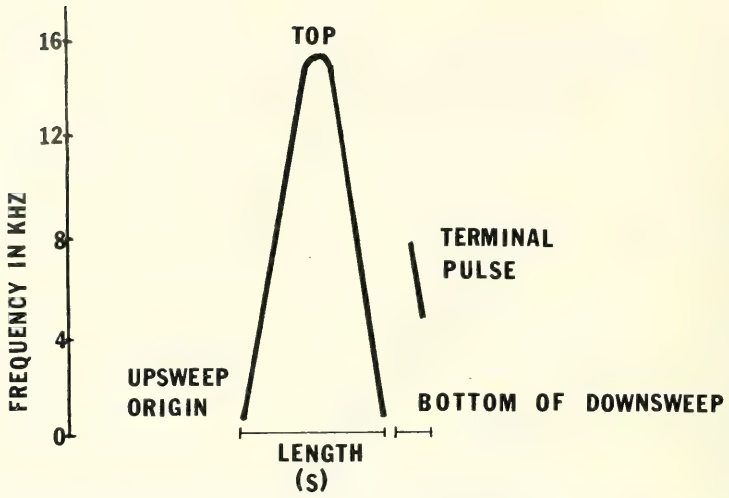

Fig. 2. Diagram of the parameters of the chip used for statistical analysis in this study. The terminal pulse was found to follow the chip of the San Jacinto populations of *Tamias merriami.*

Calls of both species were recorded in areas of sympatry of *Tamias obscurus* and *T. merriami.* Calls recorded at Columbia are from a population of *Tamias merriami* whose distribution is continuous with *T. merriami* and *T. obscurus* in the San Bernardino Mountains and allopatric with respect to *Tamias obscurus* and *T. merriami* in the San Jacinto Mountains (see Fig. 1, Hall 1981).

Methods

Spontaneous vocalizations were recorded while traversing roads and trails in the San Bernardino and San Jacinto Mountains. Calls of chipmunks were recorded from individuals spontaneously vocalizing as we approached within recording range. All chipmunks calling in this context were recorded without our knowledge of sex and weight during the same season in all of the study sites in an effort to avoid collecting data representing entirely individuals of any one age or size class. The distribution of the chipmunks and their cryptic coloration required that animals be collected and identified and bacula preserved according to Friley (1947) in the study areas prior to recording. Recording areas were selected in which species boundaries were sharp enough (see Blankenship 1985 for habitat description and distribution of the two species) in areas of sympatry (or parapatry) and recording was done away from these borders as was necessary to ensure the identity of the callers. In order to avoid recording calls repeatedly from the same individual, each area was traversed for several Km only once. These recordings were then compared with populations of *Tamias merriami* from Columbia and the San Bernardino Mountains (Brand 1970, and unpublished data).

Calls were recorded at a tapespeed of 9.5 cm/s with a Uher 4000 Report-L tape recorder and a Sennheiser MKH 404 microphone with a 60 cm parabolic reflector. Sonagrams were made from each recording using a Kay Sonagraph 6061-B set for wide band (300 Hz) analysis. Frequency and time intervals were measured from the sonagrams for all calls for the following parameters (see Fig. 2): frequency of origin of upsweep of chip, top of upsweep, bottom of downsweep, duration of

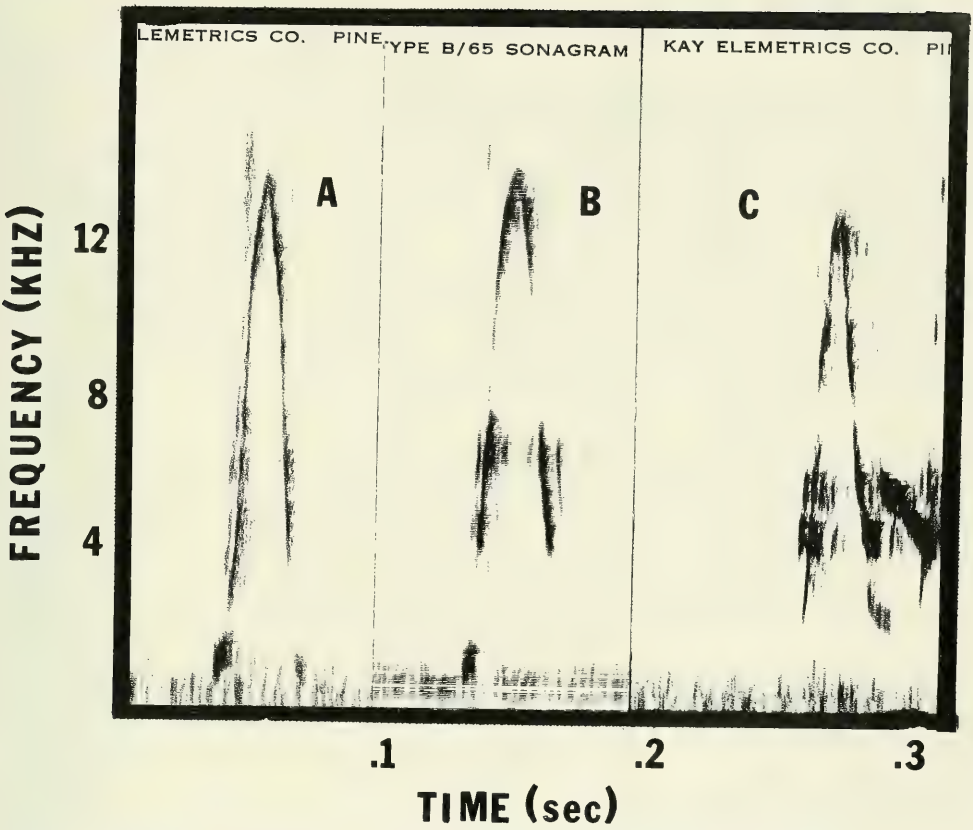

Fig. 3. Sonagrams of chips from *Tamias obscurus* in the San Bernardino Mountains (A), *Tamias obscurus* in the San Jacinto Mountains (B), and *Tamias merriami* in the San Jacinto Mountains (C).

chip, and highest and lowest frequencies of terminal pulse, if present. Interpopulation variation was analyzed using Duncan's Multiple Range Test and analysis of variance of log transformed data using an SPSS (Nie et al. 1975) program.

Results

Sonagrams of the chips of *Tamias obscurus* and *T. merriami* were both characterized by a symmetrical inverted "V" shape (Fig. 3). Based on analysis of variance (df = 4) of both species in all populations sampled, *Tamias obscurus* has a unique vocal pattern. *Tamias obscurus* and *T. merriami* differ in the frequency of the origin of the upsweep ($P < .0001$; Table 1), top of the upsweep ($P < .0001$), bottom of the downsweep ($P < .005$), and in the length of the chip in seconds ($P < .0001$; Table 2). Vocalizations of the three populations of *Tamias merriami* were distinguishable based on the length of the chip. *Tamias merriami* (Col) was different from the other populations of *T. merriami* primarily in the length of the chip and in the top of the upsweep (Table 3; Duncan's Multiple Range Test; $P < .05$). *Tamias obscurus* in both the San Bernardino and the San Jacinto mountain ranges differed from *T. merriami* in the San Bernardino Mountains primarily in the length of the chip, and from *T. merriami* in Columbia (Col) by the top of the

Table 1. Frequency range in kiloHertz of *Tamias* chips measured from sonagrams. SBD = San Bernardino, SJ = San Jacinto, Col = Columbia localities.

Species	Origin of upsweep				Top of upsweep				Bottom of downsweep			
	N	$\bar{x}$	Range	SE	N	$\bar{x}$	Range	SE	N	$\bar{x}$	Range	SE
T. obscurus (SBD)	19	1.3	1.0–1.8	0.058	19	15.0	14.1–16.0	0.183	19	2.6	1.0–5.0	0.232
T. obscurus (SJ)	31	1.4	1.0–2.0	0.058	19	14.2	12.5–16.0	0.266	31	3.2	1.0–4.8	0.189
T. merriami (SBD)	19	1.8	1.5–3.0	0.101	19	15.0	12.5–16.0	0.221	19	2.2	1.5–4.0	0.184
T. merriami (SJ)	10	2.8	1.5–4.1	0.322	10	14.8	13.8–15.5	0.178	10	1.9	1.0–4.2	0.368
T. merriami (Col)	19	1.4	1.0–1.5	0.042	19	12.6	11.5–15.0	0.326	19	2.8	1.5–3.5	0.137

Table 2. Length of *Tamias* chips in seconds, measured from sonograms. SBD = San Bernardino, SJ = San Jacinto, Col = Columbia.

Species	Length of syllable (seconds)			
	N	$\bar{x}$	Range	SE
T. obscurus (SBD)	19	0.034	0.027–.050	0.001
T. obscurus (SJ)	31	0.038	0.030–.057	0.001
T. merriami (SBD)	19	0.067	0.045–.090	0.003
T. merriami (Col)	19	0.056	0.045–.085	0.003
T. merriami (SJ)				
Chip only	11	0.037	0.027–.046	0.001
Terminal pulse only	11	0.014	0.009–.023	0.001

upsweep and the length of the chip (Table 3). The two populations of *Tamias obscurus* in the San Jacinto and San Bernardino Mountains were significantly different based on the top of the upsweep ($P < .05$; Duncan's Multiple Range Test; Table 3). The calls of sympatric *Tamias merriami* and *T. obscurus* in the San Jacinto Mountains are significantly different ($P < .05$; Duncan's Multiple Range Test) based on the origin of the upsweep (Table 3), the bottom of the downsweep (Table 3), and the terminal pulse (Table 4).

Intraspecific differences in the chips are present and, in some cases, are as great as the differences found between the two species (Table 3). Because the terminal pulse (Table 4) is unique to *Tamias merriami* (SJ), it was not included in the analysis of variance or Duncan's Multiple Range Test. For these analyses the inverted "V" shaped chip was analyzed alone. When the terminal pulse is included, as it is when the calls are naturally emitted by the chipmunk *Tamias merriami* in the San Jacinto Mountains, these calls differ even to the unaided human ear from calls of all other populations sampled of *Tamias obscurus* and *T. merriami.*

Discussion

Our data supports Brand's (1976) observation that different species of chipmunks produce unique calls. Furthermore these data show intraspecific variability in chip calls of chipmunk populations. This intraspecific variability qualifies as geographic variation rather than different dialects (Conner 1982a, b). Although learning may play a role in the perpetuation of these calls in a population, it does not detract from their possible role in mate selection. West-Eberhard (1983) has suggested that variations in behavioral traits of successful individuals in the context of mate selection may be advantageously imitated by others and may be an additional factor influencing the direction of evolution.

The significant intraspecific variability in chip calls suggests that populations of chipmunks have achieved a level of divergence in chip calls that in some cases is equivalent to differences between populations belonging to different species. *Tamias merriami* (Col) was different from all other populations in two parameters of the chip calls irrespective of whether the populations compared were allopatric or continuously distributed and conspecific. In the San Jacinto and San Bernardino Mountains sympatric species showed significant differences in two parameters of the chip call in both locations suggesting that direct selection may produce differences between these populations. However, equally significant differences also

Table 3. Statistically homogeneous subsets derived from Duncan's Multiple Range Test ($P < .05$) of log transformed means for parameters of the chip. Lines connect populations which are not significantly different from each other. P values are from Analysis of Variance of groups and are placed with the groups they represent. T.m. = *Tamias merriami,* T.o. = *Tamias obscurus,* SBD = San Bernardino, SJ = San Jacinto, Col = Columbia.

Character	P	Population				
Origin of upsweep	<.0001	T.o. (SBD) 0.1251	T.o. (SJ) 0.1476	T.m. (Col) 0.1483	T.m. (SBD) 0.2547	T.m. (SJ) 0.4184
Top of upsweep	<.0001	T.m. (Col) 1.0999	T.o. (SJ) 1.1520	T.m. (SJ) 1.1723	T.m. (SBD) 1.1744	T.o. (SBD) 1.1766
Bottom of downsweep	<.005	T.m. (SJ) 0.2788	T.m. (SBD) 0.3260	T.o. (SBD) 0.3777	T.m. (Col) 0.4472	T.o. (SJ) 0.4740
Length of chip	<.0001	T.m. (SBD) −1.1856	T.m. (Col) −1.2597	T.o. (SJ) −1.4242	T.m. (SJ) −1.4263	T.o. (SBD) −1.4726

Table 4. Frequency range in kiloHertz of the terminal pulse from chips of the San Jacinto (SJ) population of *Tamias merriami*.

	N	$\bar{x}$	Range	SE
Lowest frequency	11	4.2	3.5–6.5	0.272
Highest frequency	11	7.4	6.0–8.4	0.194

appear in allopatric species suggesting that non-direct selective pressures may also account for the differences in chip calls of these populations. West-Eberhard (1983) has suggested that distinctive signals may evolve in the absence of closely related, sympatric species producing similar signals and can be developed independently of species recognition, but may function in species recognition incidentally. The role of chip calls in mate selection is the subject of future investigation, but the intraspecific population variability in the calls of these chipmunks is consistent with expectations for the variability found in sexually selected signals (West-Eberhard 1983).

Brand (1976) noted a correlation between body weight and frequency in some, but not all, species of chipmunks that he studied; but he reported consistent and significant interspecific differences in the vocalizations of California chipmunks. Hafner and Hafner (1979) suggested some evidence was present in their study for size and call frequency relationships in Grasshopper Mice (*Onychomys*) but species discrimination by calls was still possible with 98% accuracy. They also suggested that despite the intrapopulation variability the calls could be used in mate selection seasonally.

Dunford and Davis (1975) used the absence of a terminal pulse in chips of *Tamias merriami* as one of their taxonomic criteria in the separation of a Mexican population of chipmunks. It is now evident that at least one population of *T. merriami* (San Jacinto) has terminal pulses after its chips. Vocalizations should be used only with considerable caution in taxonomic studies unless a broad study of geographical variation has been done.

The importance of behavior in reproductive isolation has been emphasized by Littlejohn (1969) and Mayr (1970). Because post-zygotic reproductive isolating mechanisms are rarely tested (Mayr 1970), behavioral reproductive isolating mechanisms may be important in mate selection of cryptic species such as these chipmunks in which sight recognition may not be adequate to ensure mating with conspecifics. Vocal signaling may help conspecifics locate each other in heavy brush and aid efforts to avoid exposure to predators during conspicuous visual displays.

Marler (1957) gives examples in birds of the effectiveness of behavioral isolating mechanisms in maintaining the genetic integrity of populations that are not otherwise reproductively isolated and must rely on behavioral signaling to reduce hybridizaton. He notes that birds living on islands have more variable calls than related birds living on continents. The reduction in species diversity apparently limits the necessity for the calls to function in reproductive isolation (Marler 1957). Mundinger (1982) observed an increased variation in some bird song patterns associated with islands; when bird distributions were continuous and breeding densities were high then song diversity was less. However, Thielcke

(1969) concluded that aberrations in bird calls on islands are not loss or intensification of differences but are due to founder effects.

Callahan (1981) reports having observed estrus female *Tamias obscurus* and *T. merriami* attracting male chipmunks from considerable distances after extensive bouts of chip calling. This observation and the presence of geographic variability in the chip calls indicates that these calls may be sexually selected and perhaps demonstrates potential for mate selection in vocalizations of chipmunks. The vocalizations of chipmunks may function in reproductive isolation, but more work should be done in order to better understand the context in which chip calls are emitted and the role they play in courtship behavior of chipmunks.

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Species Composition of Rocky Intertidal and Subtidal Fish Assemblages in Central and Northern California, British Columbia-Southeast Alaska

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Abstract.—We summarized data on species abundances for subtidal and shoreline fish assemblages from two areas in California and from the Alexander Archipelago in northern British Columbia-southeast Alaska. For the northern California and British Columbia-Alaska areas, the combined shoreline and subtidal collections were dominated numerically by cottids and stichaeids. At the central California survey area, scorpaenids were the predominant group, followed by cottids, stichaeids, pholids, and bothids. Within each region, individual species tended to occur either mostly in the intertidal/shoreline zone or mostly subtidally; rarely were species abundant in both habitats. Because intertidal species are largely confined to that habitat, populations at widely separated locations could be demographically and genetically isolated, unless gene flow (immigration) via planktonic larval dispersal occurs.

Introduction

Recent studies have provided detailed information on the species composition and, to a lesser degree, temporal changes in intertidal fish communities of temperate-zone rocky habitats (Gibson 1972; Yoshiyama 1981; Barton 1982; Grossman 1982; Yoshiyama et al. 1986), although certain aspects of this system remain to be elucidated. It is not clear, for example, whether many intertidal fish populations are merely the fringes of much larger populations centered in subtidal areas, or if the common intertidal fishes have their populations primarily restricted to that habitat. The degree to which these species are confined to the shoreline will affect their population and evolutionary dynamics; the restriction of the fishes to relatively small areas of rocky habitat will limit their population size, making them more susceptible to chance local extinctions (by both demographic and environmental stochasticity) and genetic drift. Information on this point is lacking because of the difficulty in effectively sampling rocky subtidal habitats.

If intertidal and subtidal fish assemblages are distinct, it becomes of interest to determine if they show similar structural characteristics. For example, does the composition of subtidal cryptic-demersal assemblages vary spatially (with latitude) or temporally in the same manner as intertidal fish communities (Yoshiyama et al. 1986)? In this paper we compare data condensed from reports for three shoreline/subtidal surveys on temperate, rocky-substratum fish assemblages (two data sets for California and one from British Columbia-Alaska) as a preliminary

step in comparing rocky subtidal fish assemblages. We also consider the continuity of these subtidal assemblages with their respective intertidal/shoreline counterparts, which may provide a better understanding of the organization and dynamics of intertidal fish assemblages.

Materials and Methods

The three survey areas lie within the Oregon Faunal Province of Briggs (1974) and are characterized by a temperate, cool-water fish fauna. Data on species abundances for subtidal and shoreline fish assemblages in California were collected by personnel of the California Department of Fish and Game during surveys on the shallow water fishes at two localities proposed as warm-water discharge sites for power-generating plants: Arena Cove in northern California and Diablo Cove 480 km to the south. Subtidal collections at these localities were made using SCUBA and a rotenone-based toxicant ("Chem-Fish Collector"). There were five subtidal collecting stations at Arena Cove (7.9–15.3 m depths) sampled on 17 March, 15, 17 August 1972, and 6, 8, 9 April 1973. There were six stations at Diablo Cove and the adjacent North Cove (two each within 0–3, 6.1–7.6, 18-3–21.3 m depths), sampled in May, September 1970, and January, July 1971 (Burge and Schultz 1973).

Species abundance data for Arena Cove were summarized from Gotshall et al. (1974). The Diablo Cove (plus North Cove) data presented here were condensed from a report by Burge and Schultz (1973). We tabulate the cryptic-demersal fishes: relatively small forms that rest on the bottom, in association with rocky substrates and algal cover. We exclude the highly mobile (hence difficult to sample) species that characteristically occur in the water column (e.g., anchovies and surfperches) and also most large predatory species (except the rockfish genus *Sebastes*) that moved in to feed on the smaller incapacitated fishes. We include *Sebastes,* many of which as adults are large predators, because they often are closely associated with the rocky substratum.

Capture data for northern British Columbia-southeast Alaska (Alexander Archipelago) fishes were recompiled from Peden and Wilson (1976) into a format comparable to the data for the two other localities. We list only species from their subtidal collections taken using SCUBA and toxicant (Chem-Fish), slurp gun, or "by hand" (fishes captured by gill nets or other methods are not included). Because these methods are relatively ineffective for sampling large, mobile species or those that occur primarily in the water column, those species were automatically excluded.

The data from British Columbia-Alaska and California are not entirely comparable because (1) of differences in sampling procedure (e.g., exclusive reliance on large amounts of toxicant in California), (2) the B.C.-Alaska survey covered a more extensive geographical area (>3° latitude), while the California surveys were more localized, and (3) sampling sites in B.C.-Alaska were in protected waters (e.g., leeward of islands) mostly near estuarine habitats, while the California survey areas centered around coves on the exposed coast. However, large applications of ichthyocide (California survey) allow thorough sampling of the subtidal habitat, and the B.C.-Alaska collections involved a large number (>40) of dives. Collections in each area therefore probably were representative of the small cryptic-demersal fish faunas of subtidal rocky habitats for their respective regions, and

Table 1. Relative abundances of demersal fishes of central California (Diablo Cove and Arena Cove) and British Columbia/so. Alaska. Values are proportion of total fishes collected in each depth zone (column) at abundance >20 individuals. ** denotes the distribution of species present at a locality at total abundance <20.

	Diablo Cove			Arena Cove		B.C./Alaska	
	Shore	Sub-tidal	Sub-tidal	Shore	Sub-tidal	Shore	Subtidal
	0–3 m	6.1–7.6 m	18.3–21.3 m				
Cottidae							
Artedius corallinus	.001	.067	.036		**		
Artedius creaseri		.004	.003				
Artedius fenestralis		**			.033	.001	.019
Artedius harringtoni		.007	.024	.001	.289	.002	.165
Artedius lateralis	.024	.015		.021	.001	.038	.001
Artedius meanyi					**		.008
Ascelichthys rhodorus				.009	.019	.043	.019
Blepsias cirrhosus						.039	
Clinocottus analis	.015			.007			
Clinocottus embryum				**		.022	
Clinocottus globiceps	**			.015		.047	
Young *C. globiceps* or *C. recalvus*				.024			
Enophrys bison				**	**	.013	.001
Enophrys lucas							.006
Gilbertidia sigalutes							.063
Hemilepidotus hemilepidotus						.051	.034
Hemilepidotus spinosus		.013	.009	.006	.293		
Icelinus borealis							.092
Jordania zonope		.004	.022		.037		.150
Nautichthys oculofasciatus		.002	.007		**	.001	.020
Oligocottus maculosus				.126		.223	
Oligocottus rubellio	.009	.003		.005			
Oligocottus snyderi	.012	.001		.183		.034	
Orthonopias triacis	.004	.042	.044				
Radulinus taylori							.057
Rhamphocottus richardsoni					**		.009
Scorpaenichthys marmoratus	.027	.041	.005	.015	.014		
Stichaeidae							
Anoplarchus insignis					.040	.001	.082
Anoplarchus purpurescens	.023	.001		.040		.044	.001
Cebidichthys violaceus	.008			**			
Chirolophis decoratus							.011
Chirolophis nugator		.030	.013		.085		.019
Phytichthys chirus				**	**	.043	.024
Plagiogrammus hopkinsi	.001	.009	.003				
Stichaeus punctatus							.010
Xiphister atropurpureus	.184	.001		.216		.135	.001
Xiphister mucosus	.180			.160			
Young *Xiphister* spp.				.008			
Scorpaenidae							
Sebastes carnatus		.018	.026				
Sebastes caurinus		.001	.021				.008
Sebastes chrysomelas	.023	.021	<.001		**		

Table 1. Continued.

	Diablo Cove			Arena Cove		B.C./Alaska	
	Shore	Subtidal	Subtidal	Shore	Subtidal	Shore	Subtidal
	0–3 m	6.1–7.6 m	18.3–21.3 m				
Sebastes entomelas			.010				
Sebastes melanops	.002	.006	.044	.019	.010		
Sebastes mystinus	.022	.279	.154	.007	.029		
Sebastes paucispinis	.002	.031	.010				
Sebastes pinniger		.060	.069		**		
Sebastes serranoides	.007	.024	.017				
Pholidae							
Apodichthys flavidus	.018	.001		.022		.122	<.001
Pholis clemensi					**		.006
Pholis laeta						.011	.006
Xererpes fucorum	.306	.003		.030			
Clinidae							
Gibbonsia elegans	.010	<.001					
Gibbonsia metzi	.017	.001		**			
Gibbonsia montereyensis	.062	.025		.006			
Bothidae and Pleuronectidae							
Citharichthys stigmaeus		.166	.176		**		
Pleuronichthys decurrens		.002	.008				
Hexagrammidae							
Hexagrammos decagrammus	.006	.009	.002	.016	.014		
Hexagrammos superciliosus				**			
Oxylebius pictus	.009	.059	.107		**		
Agonidae							
Anoplagonus inermis					**		.007
Pallasina barbata					**	.076	
Cyclopteridae							
Liparis dennyi							.006
Liparis florae	**	**		.019	.009	.010	.010
Liparis fucensis				<.001	.125		
Other families							
Bathymaster caeruleofasciatus							.015
Brosmophycis marginata		.014	.033				
Chilara taylori		.014	.049		**		
Coryphopterus nicholsi	<.001	.016	.052		**	.001	.020
Gobiesox maeandricus	.025	.004		.039	.003		
Rathbunella hypoplecta		.001	.056				
Ronquilis jordani							.130
Scytalina cerdale	.006	.002		**		.043	
Subtotal	3013	3298	2825	4005	792	1519	3807
Total	3072	3456	2901	4190	922	1556	4004

B.C/Alaska total includes 37 additional species (8 cottids, 4 agonids, 1 stichaeid, 1 pholid, 6 cyclopterids, 8 scorpaenids, 9 others) in numbers <20. Diablo Cove total includes 30 additional species (6 cottids, 2 stichaeids, 2 cyclopterids, 2 gobiids, 2 agonids, 7 scorpaenids, 9 others) in numbers <20 plus a new species of *Liparis* (35 individuals). Arena Cove total includes 12 additional species (4 cottids, 2 cyclopterids, 2 scorpaenids, 2 agonids, 1 pholid, 1 ammodytid) in numbers <20.

Table 2. Summary of fishes by family, shoreline and subtidal collections combined, from Table 1. Only species collected in abundance >20 individuals are included.

Family	Number of species			Proportion of total individuals[1]		
	Diablo Cove	Point Arena	B.C./ Alaska	Diablo Cove	Point Arena	B.C./ Alaska
Cottidae	12	13	19	.15	.46	.61
Stichaeidae	6	5	7	.15	.38	.17
Scorpaenidae	9	2	1	.29	.03	.01
Pholidae	2	2	3	.11	.04	.05
Clinidae	3	1		.04	.01	
Hexagrammidae	2	1		.06	.02	
Agonidae			2			.03
Cyclopteridae		2	2		.04	.01
Bothidae	1			.11		
Pleuronectidae	1			*		
Gobiesocidae	1	1		.01	.03	
Scytalinidae	1		1	*		.01
Bathymasteridae	1		2	.02		.10
Gobiidae	1		1	.02		.01
Ophidiidae	1			.02		
Bythitidae	1			.01		
Total individuals				9136	4797	5326

[1] * denotes proportion <0.01.

general comparisons with regard to relative abundances of these species appear valid. Because sampling in British Columbia-Alaska did not rely on large-scale applications of ichthyocide, it is likely that large and mobile *Sebastes* spp. (Scorpaenidae) were more poorly sampled than in California, where heavy use of toxicant undoubtedly facilitated their capture. Therefore, although we include data for this group from British Columbia-Alaska for completeness, quantitative comparisons of the scorpaenid data between this and the other two surveys probably would not be valid. The above limitations on comparability of the three surveys require caution in making comparisons between the surveyed faunas, and so we emphasize only qualitative similarities or differences between them. However, sampling protocol within surveys was consistent so that it is valid to make quantitative comparisons within a single survey—viz., comparing distributional patterns of species between shoreline and subtidal habitats.

Results and Discussion

The data for the three surveys indicate a general similarity between regions, with cottids and stichaeids as important faunal components in all three areas (Tables 1, 2) Scorpaenids were strongly represented in Diablo Cove, but this probably was due to differences in collecting procedures (Methods). Of the remaining families, only the pholids were consistently represented in all three areas.

At the species level, there were some notable differences between the faunas. In British Columbia-Alaska, the dominant subtidal cottids were *Artedius harringtoni, Icelinus borealis,* and *Jordania zonope*; at Arena Cove they were *A. harringtoni* and *Hemilepidotus spinosus,* while at Diablo Cove they were *A. corallinus, Orthonopias triacis,* and *Scorpaenichthys marmoratus.* The dominant

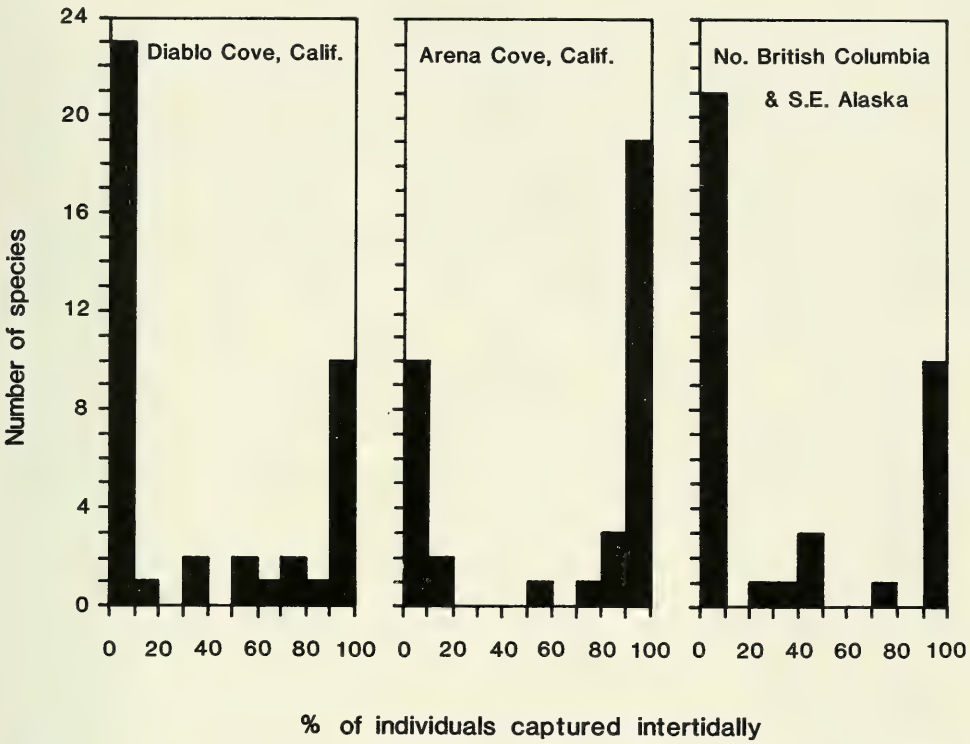

Fig. 1. Distribution of species between intertidal and subtidal zones. Bars indicate the numbers of species that had the specified percentage of their captures in the intertidal zone.

stichaeids were *Anoplarchus insignis* (B.C.-Alaska), *Chirolophis nugator* and *A. insignis* (Arena Cove), and *C. nugator* (Diablo Cove), and the major scorpaenids were *Sebastes caurinus* (B.C.-Alaska), *S. flavidus, S. mystinus* (Arena Cove), and *S. mystinus* and *S. pinniger* (Diablo Cove). Ronquils (Bathymasteridae) were abundant in B.C.-Alaska and at Diablo Cove, but not at Arena Cove, and cusk eels and brotulas (Ophidiidae and Bythitidae) were collected in moderate numbers at Diablo Cove but not in the other two surveys.

The general picture conveyed by the subtidal collections resembles that shown by the rocky intertidal fish faunas that occur along much of this same geographical range (Yoshiyama et al. 1986). There was overall similarity between the surveyed areas in the major groups of fishes present (e.g., cottids, stichaeids, scorpaenids), but there was a definite latitudinal change in species composition of the fauna.

Within each of the three surveys, species abundances generally were different between shoreline and deeper subtidal collections (Table 1). At Diablo Cove, the shoreline (including intertidal) collections were dominated by the eel blennies *Xiphister atropurpureus, X. mucosus,* and *Xererpes fucorum,* while these species were rare or absent in the subtidal collections. Conversely, the bothid flatfish *Citharichthys stigmaeus* and the hexagrammid *Oxylebius pictus* were much more abundant in the subtidal areas than shoreward. Most of the other species also were concentrated in either the shoreline or deeper subtidal areas. The same was true for B.C.-Alaska (e.g., *Artedius harringtoni, Icelinus borealis,* and *Jordania*

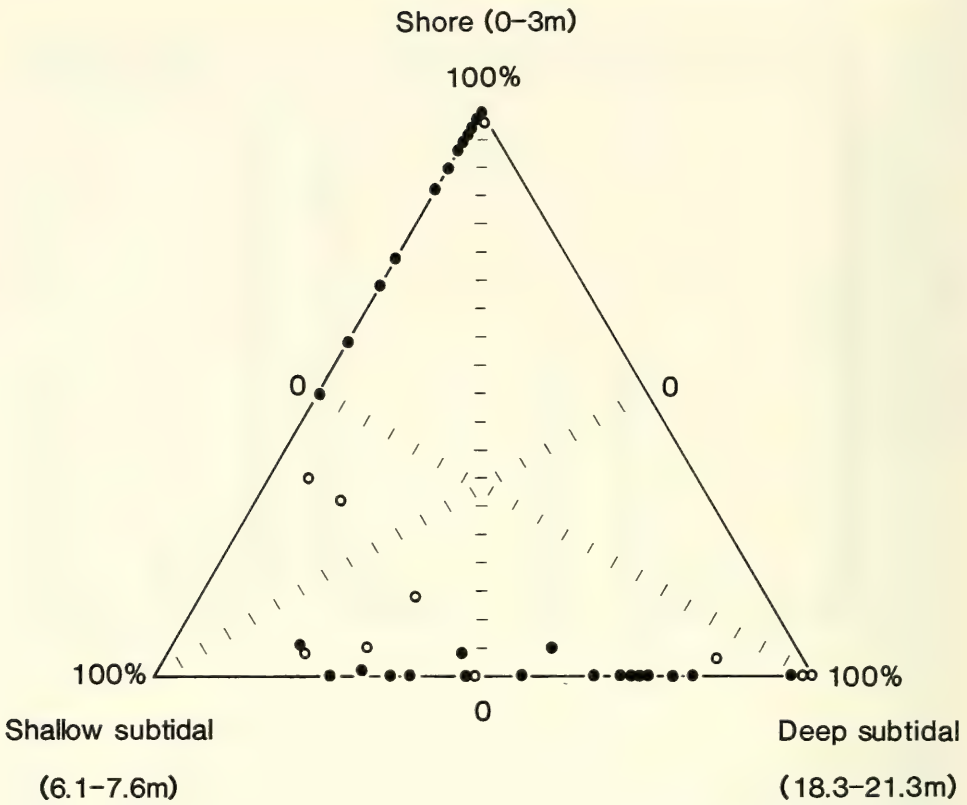

Fig. 2. Proportionate abundances of the 42 most common species in three depth zones (0–3 m, 6.1–7.6 m, 18.3–21.3 m) at Diablo Cove, California. Each apex of the triangle corresponds to 100% of the captures in the designated depth zone. Axis for each depth zone extends from apex (100%) to midpoint of opposite side of the triangle (0%). Species with maximum total length <50 cm are represented by solid dots, larger species by circles.

zonope primarily subtidal; *Xiphister atropurpureus* and *Apodichthys flavidus* mainly on the shoreline) and also for Arena Cove. This pattern of depthwise distribution yielded a U-shaped histogram when we plotted the frequency distribution of species against specified percentages of captures in the intertidal zone (Fig. 1; e.g., at Diablo Cove, 23 species were captured 0–10% of the time in the intertidal zone, and 10 species were captured intertidally at frequencies of 90–100%). Thus, most of the species common in the intertidal (shoreline) zone evidently do not have populations extending substantially into subtidal areas.

Plotting the data for Diablo Cove as proportions (of captures) on triangular coordinates (Fig. 2) illustrates how individual species are distributed among the three depth zones sampled. There is a cluster of species captured almost entirely in the intertidal zone (top apex of triangle), with a few more distributed more evenly between the intertidal and shallow subtidal zones (left side of triangle). Species caught mostly subtidally (base of triangle) were distributed to varying degrees between the shallow subtidal and deep subtidal zones—i.e., few were caught exclusively in the deep subtidal and none exclusively in the shallow subtidal. Only a few species were caught in all three depth zones in substantial numbers

(Fig. 2, open circles in the interior of triangle), and these were large species with adults located primarily subtidally and with juveniles in the intertidal zone (e.g., *Scorpaenichthys marmoratus, Hexagrammos decagrammus, Sebastes* spp.). Aside from these large species, the remaining small forms were captured mainly in one or two depth zones (Fig. 2, solid dots).

Our conclusion that the shoreline/intertidal assemblages are essentially distinct from the subtidal assemblages at the three localities examined was foreshadowed by Miles' (1918) similar observation that "individuals taken at points more than 1 meter below lowest tide were usually of a different species than those found higher up." However, the degree of discontinuity between intertidal and subtidal assemblages probably varies from one place to another, depending upon environmental characteristics and the taxa involved.

It might seem from the discontinuity between the intertidal and subtidal assemblages examined that for some species intertidal populations at widely separated localities constitute distinct stocks—in the sense that individuals within a "stock" interbreed mainly among themselves. Certain features of adult intertidal fishes indicate restricted dispersal abilities or tendencies—e.g., stichaeids and pholids lack gas bladders and have elongated shapes poorly suited for sustained swimming, and some cottids show strong fidelity or homing to specific tidepools (Williams 1957; Green 1971, 1973). However, for cottids and stichaeids, current-mediated dispersal of the planktonic larvae along the coast could prevent the genetic isolation of spatially separated populations. Our recent work on the distribution of allozymic variants in cottid populations on the open coast indicates that significant gene flow (hence movement of individuals) does occur in some species, presumably during the larval phase (Yoshiyama and Sassaman 1987). It is nonetheless likely that in certain situations, such as in sheltered areas, even the dispersal of planktonic larvae is restricted since Marliave (1986) has shown that larvae of some intertidal fishes actively maintain position close to the shoreline, thereby avoiding alongshore drift.

For most of the common intertidal species there was no detectable shift in distribution to the subtidal zone at southern latitudes. *Artedius lateralis* seemed to be shifted somewhat toward the subtidal at Diablo Cove, but this may have been partly an artifact of some subtidal collection stations at Diablo Cove being situated in shallower depths (6.1 m+) than at Arena Cove (7.9 m+). Some degree of "subtidal submergence" nonetheless may occur, but larger sample sizes and more detailed depthwise sampling schemes are needed to clarify this point.

Finally, Diablo Cove is the site of a presently operative nuclear power plant which was constructed subsequent to the 1970–1971 faunal survey. Warm-water discharge from the plant possibly has altered the species composition of the shallow water fish fauna at this locality, and further sampling would be instructive to show whether the fish fauna has changed in response to this clearly-defined environmental change.

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Structure of Internal Varices in the Shell of *Micrarionta rufocincta* and Other Helminthoglyptidae (Gastropoda: Pulmonata)

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Abstract.—One or more internal varices are present in about half of all *Micrarionta rufocincta* shells examined, usually associated with the strong growth lines that represent interruptions of helical growth. Shell structure in *M. rufocincta* consists of an outer, radial crossed-lamellar layer; a middle, concentric crossed-lamellar layer; and an inner, radial crossed-lamellar layer. Deposition of the inner layer lags 1–2 mm behind deposition of the outer and middle layers. Most of the thickness of a varix results from an increase in the depth of the middle layer. Similar varices are found in the Californian *Micrarionta beatula, M. feralis, Helminthoglypta sonoma, H. carpenteri,* and *H. petricola* and the West Indian *Hemitrochus varians* and *Polymita picta.* In *M. rufocincta,* varix formation occurs shortly before the onset of dry season estivation. Its main function is probably to strengthen the lip of the juvenile shell and provide greater attachment area for mucous seals during times when the threat of desiccation is greatest.

In many marine gastropods, the functionally optimal shell configuration entails a periodic departure from regular helical form. Members of the Cassidae, Cymatiidae, Bursidae, and Muricidae interrupt the helix at various intervals to add a thickened or reflected apertural varix (Linsley and Javidpour 1980). In terrestrial gastropods, departures from regular helical form are predominantly confined to a terminal phase of growth, in which the whorl trajectory, diameter, or cross-section may be modified and the aperture augmented with a flange or other form of thickening. Modifications during the course of neanic growth are usually relatively superficial and recur at frequent, small intervals, as with the axial ribs of *Cerion* (Gould and Woodruff 1978) or *Anguispira* (Jones 1935).

Land snails of the genus *Micrarionta* Ancey, 1880, terminate helical shell growth with a thickened and reflected lip as usual in most west American Helminthoglyptidae. *Micrarionta rufocincta* (Newcomb, 1864) from Santa Catalina Island, California, additionally modifies the shell by producing from one to four internal radial thickenings or varices. (The term *varix*—plural, *varices*—has usually been applied to external radial thickenings of gastropod shells. There seems no reason not to extend its meaning to similar structures located inside the shell.) These structures have not been recognized previously in west American genera. Pilsbry (1939:206) noted "buff growth-rest stripes on the base" of *M. rufocincta* but apparently did not realize that these stripes are the external traces of internal thickenings. In the West Indian helminthoglyptid genera *Hemitrochus* Swainson,

Table 1. Incidence of internal varices in *Micrarionta rufocincta* examined in this study.

Sample	Number of varices per shell				
	0	1	2	3	4
SMBNH 33896					
Adult (n = 16)	2	11	3	0	0
Juvenile (n = 35)	24	9	2	0	0
CAS pooled sample					
Adult (n = 206)	93	81	22	9	1

1840, and *Polymita* Beck, 1837, varices are formed both during and at the end of helical growth.

This paper describes the structure of varices in these three genera as seen in section under scanning electron microscopy. Data on the incidence and positioning of varices in *M. rufocincta* and an interpretation of their function are presented. (The taxonomic distinction between *M. rufocincta* and *Micrarionta beatula* Cockerell, 1929, here treated as separate species, will be discussed in a review of the land mollusks of the California islands being prepared by F. G. Hochberg and the author.)

Materials and Methods

Specimens of *Micrarionta rufocincta* were collected on Santa Catalina Island in March 1984; additional *M. rufocincta* and shells of other helminthoglyptid species were examined in the collections of the California Academy of Sciences (CAS) and Santa Barbara Museum of Natural History (SBMNH). The number and position of varices were determined by viewing shells with transmitted light. Number of whorls was measured to the nearest tenth of a whorl by the method of Diver (1932). Shell diameter was measured to the nearest 0.1 mm with hand-held calipers, perpendicular to the axis of coiling, excluding the expanded lip of adult shells. For structural analysis, shells were broken with pliers until fracture surfaces normal to the varices were obtained. The fragments were cleaned of debris in water in an ultrasonic cleaner, mounted on stubs with household cement ("Duco") and coated with Au to a thickness of 125 Å for scanning electron microscopy; SEM photos were taken in the CAS Department of Entomology with a Hitachi S-520 scanning electron microscope. Voucher specimens are on deposit in CAS and SBMNH.

Radial crossed-lamellar structure is that in which individual first-order lamellae intersect the growing shell margin perpendicularly or at high angle; concentric crossed-lamellar structure is that in which first-order lamellae approximately parallel the margin (MacClintock 1967).

Observations

In a randomly collected sample of 51 *Micrarionta rufocincta* from Fourth-of-July Canyon, Santa Catalina Island (SBMNH 33896, collected 13 March 1984), 14 of 16 adult shells and 11 of 35 juvenile shells had one or more varices; incidence of the varices is summarized in Table 1. The varices were located from the 3.4- to 5.8-whorl position. Shells of less than 4.0 whorls had no varices. In juvenile

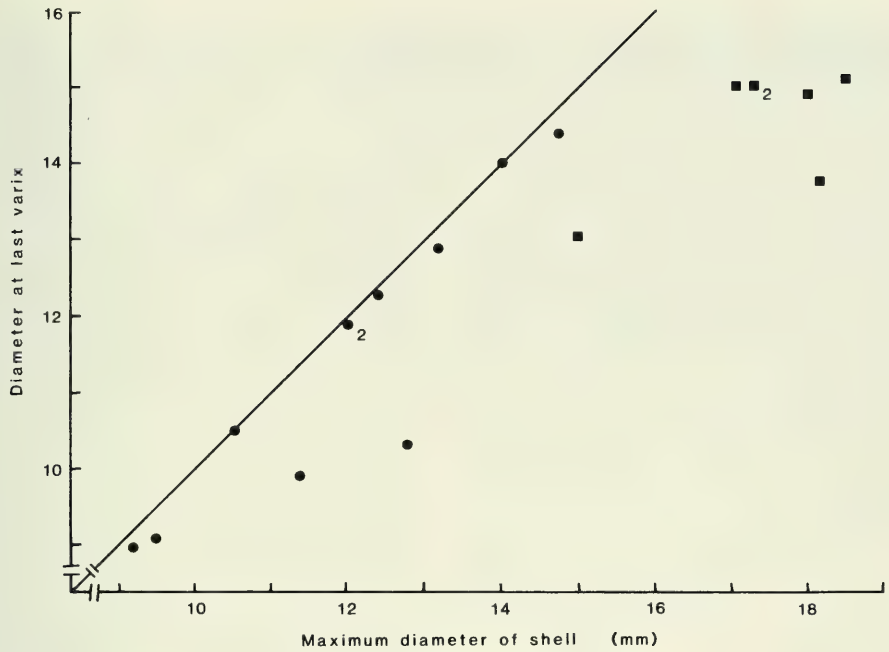
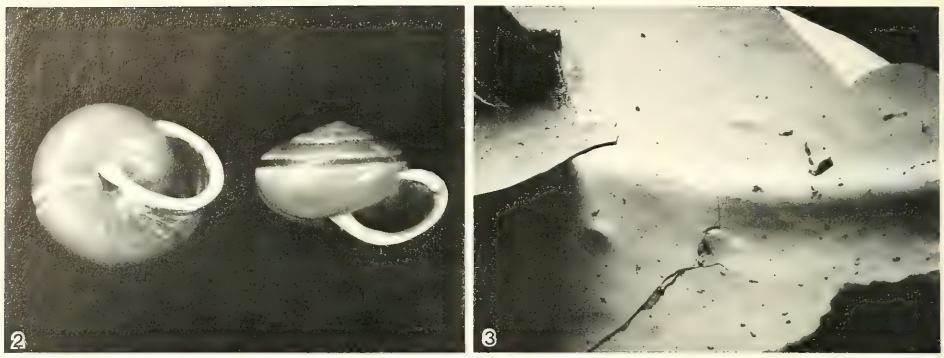


Fig. 1. *Micrarionta rufocincta* (Newcomb), SBMNH 33896: shell diameter at position of last varix plotted against maximum shell diameter. Circles, juvenile shells; squares, adult shells. Distance to right of bisector indicates increase in diameter between varix and lip. Subscripts (2) indicate multiple specimens.

shells of 4.0–5.5 whorls there were 0.0–0.6 (mean 0.08) whorls of growth between the last varix and the edge of the lip. These specimens showed an increase in diameter of 0.0–2.5 mm between varix and lip (Fig. 1). In adult shells, which ranged from 5.8 to 6.25 whorls, there were 0.1–1.5 (mean 0.56) whorls of growth between the last varix and the terminally reflected lip and an increase in diameter of 1.9–4.5 mm (Fig. 1; the diameter of seven adult shells, broken by predators, could not be measured, so the illustrated sample consists of seven adults, 11 juveniles). The varices are smooth, whitish, and of roughly uniform thickness throughout (Figs. 2, 3). They extend from suture to columella, parallel to the growth lines, but are absent from the parietal region.

In the largest sample available, 206 adult shells of *M. rufocincta* in the CAS collection, 113 (55%) had one or more varices; their incidence is summarized in Table 1. These shells do not represent population samples; they are pooled from older collections and not localized farther than "Catalina." Nevertheless there is no reason to suspect selection by collectors for or against the presence of varices. The varices were located from the 4.0- to 6.0-whorl position, in shells having 5.2–6.5 total whorls. Nearly all were within 0.1 whorl behind one of the strong growth lines that represent interruptions of helical growth. There were 0.1–1.8 (mean 0.70) whorls (generally representing one season's increment of growth) between a varix and the adult lip. The single four-varicose specimen (5.7 total whorls) had varices at 4.5, 5.3, 5.4, and 5.5 whorls.

Shell structure in *Micrarionta rufocincta* consists of: (1) an outer, radial crossed-



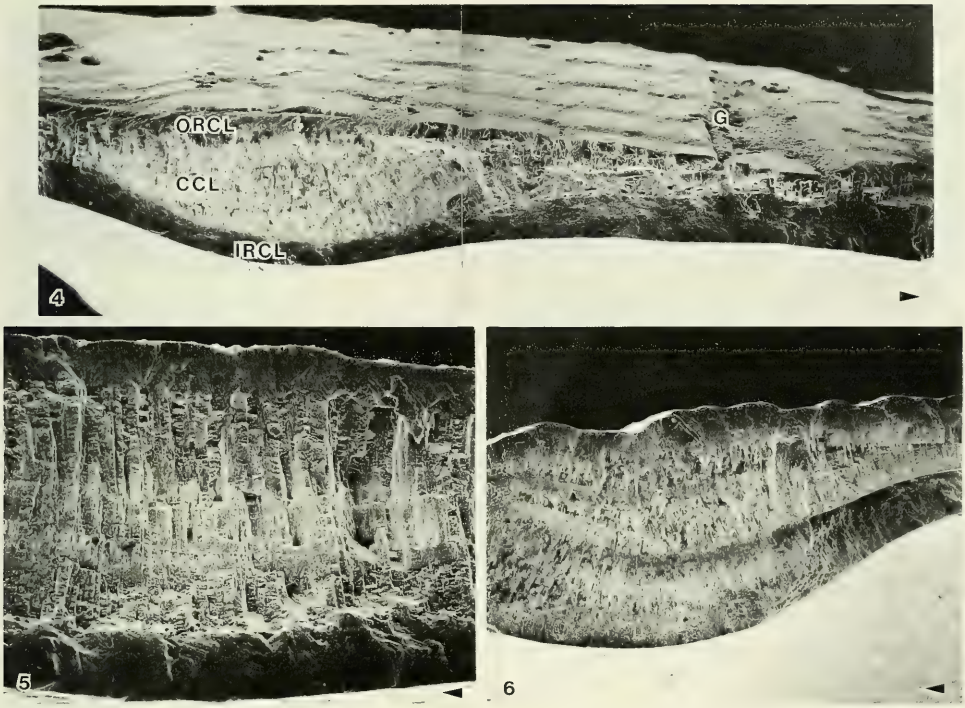
Figs. 2–3. *Micrarionta rufocincta.* 2, Shells (SBMNH 33896), basal and apertural views, diameter 17.3 mm; varix at position of light streak to left of umbilicus. 3, Part of varix extending across base of body whorl (CAS 051774), ×10.

lamellar layer with first-order lamellae perpendicular to growth lines and parallel to the direction of helical growth; (2) a middle, concentric crossed-lamellar layer with first-order lamellae oriented at right angles to the first and perpendicular to the direction of helical growth; and (3) an inner, radial crossed-lamellar layer with first-order lamellae again perpendicular to the growth lines (Figs. 4–6). Second-order lamellae of the radial crossed-lamellar layers dip at angles of 28°–38° to the inner and outer surfaces of the shell. The contact between the outer and middle layers is gradational, with the first-order lamellae undergoing a 90° rotation in the plane of the shell surface; the contact between the middle and inner layers is sharp and unconformable. In areas of normal, completed growth, the inner and middle layers each make up about 40% of the thickness of the shell; the outer layer makes up about 20%. In general, where the outer two layers are thin, as at the beginning of a new growth increment, the inner layer is thicker so that the final shell thickness remains relatively constant.

In juvenile shells the inner layer does not reach the growing margin of the aperture but thins to a feather edge within 1–2 mm behind it. The unconformity at the end of one helical growth increment and the beginning of another (Fig. 4, directly below the strong growth line, G) affects the outer and middle layers only. The inner layer passes under it without a break.

Most of the thickness of a varix results from an increase in the depth of the middle, concentric crossed-lamellar layer. Several separate episodes of shell deposition may go into producing the final thickness: minor unconformities divide the middle layer into subordinate layers (four visible in Fig. 6) and the inner subordinate layers "drape" over the outer ones (Figs. 4, 6). In addition, the subordinate layers become thicker toward the center of the varix. No shells were found with the varix partly formed, suggesting that, as Linsley and Javidpour (1980) concluded for marine gastropods, varix formation takes place very rapidly.

All other species of *Micrarionta* were examined for the presence of varices. Twenty-three (9%) of 261 specimens of *Micrarionta beatula* Cockerell 1929, from Santa Catalina Island, had a single varix; one had two varices spaced about 0.1 whorl apart. The varices had the same structure as those in *M. rufocincta* but were smaller, in proportion to the smaller, thinner shell of *M. beatula.* They were



Figs. 4–6. *Micrarionta rufocincta,* sections of varices. 4, View toward base of shell (CAS 051775), ×75. 5, View toward apex of shell (CAS 051776), ×200. 6, View toward apex of shell (CAS 051776), ×75. Arrowheads indicate direction of helical growth; exterior of shell at top in all section photos. Abbreviations: G = strong growth line; CCL = concentric crossed-lamellar layer; IRCL = inner radial crossed-lamellar layer; ORCL = outer radial crossed-lamellar layer.

similarly positioned, behind strong growth lines. Seventeen (12%) of 141 specimens of *Micrarionta feralis* (Hemphill, 1901), from San Nicolas Island, had a single varix; one had two varices spaced less than 0.1 whorl apart. They had the same structure as those in *M. rufocincta* and were positioned behind strong growth lines. I found no varices in *M. facta* (Newcomb, 1864), *M. gabbi* (Newcomb, 1864), *M. guadalupiana* (Pilsbry and Vanatta, 1898), *M. opuntia* Roth, 1975, or *M. sodalis* (Hemphill, 1901).

Similar varices occasionally occur in three species of the predominantly Californian genus *Helminthoglypta*: *H. carpenteri* (Newcomb, 1861), *H. petricola* (Berry, 1916), and *H. sonoma* Pilsbry, 1937. In the material I examined, there was no more than one varix per shell.

Internal varices in *Hemitrochus varians* (Menke, 1829) and *Polymita picta* (Born, 1780) are similar in form and structure to those of *M. rufocincta* (Figs. 7, 8). The shells of these species are composed of inner and outer radial crossed-lamellar layers with a middle concentric crossed-lamellar layer; augmentation of the middle layer accounts for most of the extra thickness at a varix. Varices produced during and at the end of helical growth have the same basic structure. In adult *P. picta* the middle layer ends abruptly, with little diminution, on the forward edge of the terminal varix. The inner layer curves outward over this layer,

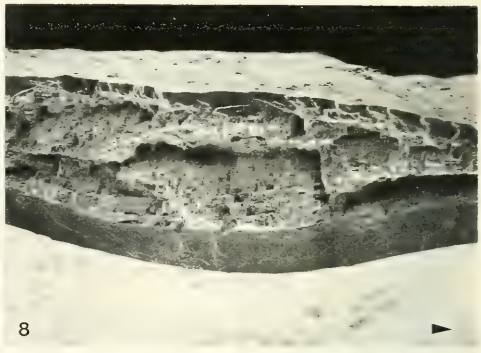


Fig. 7. *Polymita picta* (Born), section of terminal varix, view toward base of shell (CAS 051777), ×50; break at right side of photograph is an artifact. Fig. 8. *Hemitrochus varians* (Menke), section of terminal varix, view toward base of shell (CAS 051778), ×50. Arrowheads indicate direction of helical growth; exterior of shell at top of photos.

contacting the outer layer and capping the lip with a smoothly rounded edge. In adult *H. varians* all layers gradually thin toward the lip. The middle layer pinches out altogether about 0.06 mm from the lip. The inner layer contacts and sometimes extends slightly beyond the end of the outer layer.

Discussion

The varices of helminthoglyptids are not large enough to qualify as "barriers" (*sensu* Solem 1972) to exclude predators or directly retard water loss through the aperture. The fact that they extend over the exposed, outboard surfaces of the whorl but are absent from the parietal region suggests that they are involved in strengthening the shell against some externally applied stress.

Thick shell of crossed-lamellar structure is more resistant to crushing than is thinner shell (Vermeij and Currey 1980). However, at least in the land snail *Cerion,* shell thickness between ribs is more significant than thickness at a rib or rib density in determining a shell's ability to resist fracture (Gould and Woodruff 1978). It is unlikely therefore that *general* shell reinforcement is the most significant function of internal varices in *Micrarionta.*

The major shell-breaking predators of *Micrarionta* on the Channel Islands are rodents (principally deermice, *Peromyscus maniculatus*). Broken shells from the Fourth-of-July Canyon sample show two types of break, both sometimes present on the same shell: (1) irregular, "wandering" edges, often with small chips or concave facets, which follow no structural pattern in the shell itself; and (2) straighter edges that after intersecting a growth line or suture follow that zone of structural weakness in the shell. The first type is clearly the result of attack by gnawing and often passes right through a varix. The second type, evidently the result of a blow or other stress, rarely passes through a varix, but neither is predation averted, as the shell fails at other weak points. I have found no specimens with repaired breaks indicating survival from such an attack. The varices of *M. rufocincta* are too sparse and too local to amount to much of a defense against rodent predation.

As Solem (1959) noted, an unreflected aperture in land snails seems to be an

adaptation aiding attachment to solid objects such as tree limbs. Arboreal snails of the genera *Liguus, Drymaeus,* and *Orthalicus* (all of which seal strongly to tree trunks or limbs) have unreflected apertures and often an internal varix just back of the lip. The special virtue of a varix in this position may be to strengthen this otherwise delicate part of the shell against dislodgement. It also enlarges the area of shell to which a mucous seal can attach.

The climate of coastal southern California is Mediterranean, with warm, dry summers and most precipitation concentrated in the winter months. At Avalon, Santa Catalina Island, normal annual precipitation is 32.74 cm, only 2.59 cm of it falling from May through October (Elford 1970). At this dry season *Micrarionta* estivate and deposition of shell at the lip edge ceases. Inactivity and mucous seal formation can be induced at other times by exposure to dry conditions (Roth, personal observations). Desiccation, possibly the main cause of land snail death on a worldwide basis (Solem 1984), is the major threat to *Micrarionta* at these times.

Varices are evidently deposited at the start of or just prior to such periods of inactivity. The sample of *M. rufocincta* from Fourth-of-July Canyon preserves shells in their state of growth at the close of the wet season. These snails were sealed when collected and, barring a major rainstorm, presumably would have remained that way until the autumn rains. The specimens along the bisector in Fig. 1 are those that have recently completed this sequence of varix deposition. In the field, estivating adult *Micrarionta* are often found free in the litter with an epiphragm completely closing the aperture. Estivating juveniles typically seal to a solid object. Most varices are positioned where they would strengthen the lip of juvenile snails in estivation and improve the mucous seal by enlarging its base of attachment.

Deposition of the inner layer, which builds up the ultimate thickness of the shell, probably follows when the snails resume activity at the next wet season.

The net effect is that of a system in which the middle shell layer, "available" at the growing margin, is adopted to produce a temporary strengthening member. The inner layer, lagging 1–2 mm behind the outer and middle layers, comes in later, building up full shell thickness without the weakness of an unconformity at the site of the growth break.

Polymita is unusual among Helminthoglyptidae in concluding helical growth with an internal varix instead of a reflected lip. It is also unusual in being arboreal. *P. picta* occurs on forested terraces inland from Punta Maisí, Oriente Province, Cuba. Normal annual rainfall within its range is 114–152 cm but winters are relatively dry (Roth 1984). Like *Micrarionta, Polymita* may often need to maintain an unbroken seal against desiccation for weeks or months at a time.

The similarity of the terminal varix in *P. picta* to those formed earlier in its ontogeny suggests that it could have evolved by truncation of the developmental program that leads in most Helminthoglyptidae to a reflected lip. Some stratigraphic evidence in support of this proposition is available: the Eocene *Polymita texana* Roth (1984) has both a terminal varix and a weakly reflected outer lip.

Acknowledgments

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Research Notes

Copulatory Behavior of the Dusky-footed Woodrat (*Neotoma fuscipes*)

Dewsbury (1972) provided an outline for classification of the copulatory patterns of mammals. According to this schema, a species may or may not display a lock or tie which holds the penis firmly in the vagina. *Neotoma albigula, N. floridana,* and *N. micropus* all display a locking pattern during copulation (Dewsbury 1974a, b; Spencer 1968). *Neotoma cinerea* (Escherich 1981) and *N. lepida* (Estep and Dewsbury 1976) do not have this pattern.

Dewsbury (1974a) proposed that patterns of copulatory behavior of simple-baculum muroid rodents may be associated with morphological adaptations (e.g., a locking pattern is expected in a species possessing a glans penis that is thick relative to its length). Hooper (1960) developed a phallus size ratio which equals glans greatest diameter/length × 100. Two locking species, *N. albigula* and *N. floridana,* have intermediate values, equalling 47 and 53, respectively. Two non-locking species, *N. lepida* and *N. cinerea,* possess phalli with low ratios equal to 11 and 23, respectively (Hooper 1960). The penis of *N. fuscipes* has a relatively small baculum, poorly developed penile spines, and a high diameter/length ratio of 79 (Hooper 1960). The copulatory behavior of this species is virtually unknown. The only information about its mating comes from Wood (1935) who observed that "Eight copulations, each lasting about five seconds took place within less than 10 minutes." Wood did not time copulatory motor patterns nor make a detailed analysis of copulatory behavior. The present study provides an initial descriptive analysis of the copulatory behavior of the dusky-footed woodrat (*N. fuscipes*).

Animals were live-trapped in the Santa Ana, Santa Monica, and Tehachapi mountains of southern California and housed individually in cages provided with nesting materials (twigs and shredded paper) and a layer of sandy soil. Seventeen rats (8 males and 9 females) were used as test subjects. They were fed Purina rat chow, oranges, and carrots. Rats were kept on 16:8 light-dark cycle. Tests were run approximately 3 hours into the dark period. Behavioral observations, excluding those episodes filmed, were made with a red light (60 W bulb) placed approximately 25 cm above the test chamber. The test chambers were approximately 25 cm high, 50 cm long, and 25 cm deep. The observer sat 3 m away. One-hundred and thirty-four copulations were filmed using a Super 8 mm Bauer S108 movie camera with an fl.8/7.5–60 mm zoom close-up lens and Kodak Type G Ektachrome 160 film. Hormones were injected intramuscularly into each female to initiate behavioral estrus. Estradiol-benzoate (0.015 gm in 1.5 cc of peanut oil) was injected approximately 72 h before the test, and progesterone (0.15 gm in 1.5 cc of peanut oil) was injected 3–5 h before the test. Several tests were run without the aid of hormones. No apparent behavioral differences were observed between injected and non-injected females. Photoperiod alone may have been a sufficient stimulus to initiate behavioral estrus. A male and female were introduced simultaneously into the test chamber. Tests were terminated if copulation had not

occurred within the first 40 minutes. Thirty minutes were allowed after the last copulation before a test was terminated.

In all cases but one (N = 23), males initiated the copulatory sequences. The dominant animal approached the subordinate partner and tail-rattled (Linsdale and Tevis 1951). Subsequent to tail-rattling by the dominant animal, the subordinate usually moved close and turned tail-first to the male. During a successful mating episode chasing was rare. The female exhibited lordosis in which she planted her feet, raised her head and perineum, depressed her lumbar region and deflected her tail. This position was described for other rodents by Dewsbury (1967). Mean latency to attain first intromission was 296 seconds (range = 25–1580). Copulations were observed in 23 of 105 test sequences, with as many as 71 intromissions per testing period. More than 900 copulations were observed. Mean length of intromission was 2.4 seconds (range = 0.5–4.5) and was always terminated by the female walking out of the copulatory position. As the female moved away from the male no locking between the individuals was observed. Following intromissions, males and females bent down and orally groomed their genital areas. Mean inter-intromission period for multiple intromissions was 53 seconds (range = 14–840). *Neotoma fuscipes* did not lock during copulation and did not display intravaginal thrusting. Males can potentially ejaculate on a single insertion and do attain multiple ejaculations during a single test period (Dial 1978). These characteristics follow pattern #15 of Dewsbury (1972).

Ancillary tests were done with three lactating females. Tests were performed the evening following their capture from the field. No hormones were administered to these animals. Nine tests were conducted using four different males. Upon approach by a male, each female immediately lay down on her back and remained motionless. If the male persistently attempted to initiate an interaction the female squealed frequently and loudly.

Dewsbury (1974a) explains that locking species must achieve a firm connection between penis and vagina, and the penis of locking species might be expected to be thicker than those of non-locking species. *Neotoma* that possess a *uniformly* wide phallus (*N. albigula* and *N. floridana*) attain a lock during intromission, consistent with Dewsbury's (1972) prediction. The penis of *N. fuscipes* is wider in its expanded midsection than any other species of woodrat described (see Hooper 1960), yet it does not lock during copulation. Therefore, penis greatest diameter/length ratio alone may not be an adequate morphological feature to predict locking. Instead, overall shape of the phallus may be more instructive. In addition, the baculum of *N. fuscipes* is very small and would lend minimal structural support to the penis, while locking species of *Neotoma* possess relatively stout bacula (Hooper 1960).

Dewsbury (1972) suggested that locking behavior might be correlated with copulation within a structural refuge, such as a woodrat den. Species that establish a lock might be more vulnerable to predation, if exposed, compared to species which separate quickly. *Neotoma lepida,* a non-locking species, constructs relatively small dens (Cameron 1971), while *N. albigula* (Findley 1958) and *N. floridana* (Rainey 1956), locking species, construct large dens. *Neotoma fuscipes,* however, are known to build some of the largest dens (Linsdale and Tevis 1951) but are not known to lock during intromission (Dial 1978). The correlation between habitat and copulatory behavior, therefore, remains unclear.

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Accelerator Mass Spectrometry ^{14}C Determinations on Human Remains from Schuiling Cave, Mojave Desert, California

A right temporal bone of *Homo sapiens* recovered from the fossiliferous deposits in Schuiling Cave, Mojave Desert, California, previously thought to be late Pleistocene in age, is now known to be Holocene. Although stratigraphically associated with and exhibiting a similar degree of fossilization when compared with the remains of extinct taxa recovered from the middle levels of the cave, an organic fraction of the specimen has yielded a ^{14}C determination indicating a middle Holocene age. Amino acid composition data obtained on the human bone is consistent with a Holocene age.

Schuiling Cave was discovered on the east slope of the Newberry Mountains, central San Bernardino County by R. Sayles and W. Schuiling in 1953. A joint excavation by the San Bernardino County Museum and the Natural History Museum of Los Angeles County (LACM) in 1955 (Smith 1955) recovered an assemblage of fossils including five extinct vertebrate taxa (Downs et al. 1959). The human specimen (LACM 47722) and additional taxa were later identified in the LACM collections by Jefferson (1983).

Previous estimates of a late Pleistocene, Rancholabrean age for the fossiliferous, fluvial sedimentary deposits in the cave were primarily based on an alluvial and erosional sequence that was thought to have, in part, occurred in response to climatic changes across the Pleistocene/Holocene boundary (Jefferson 1983). However, some time prior to the preservation/permineralization of the vertebrate remains, the human specimen had to have been intruded into mid-cave levels by a presently unknown mechanism. Apparently, arroyo formation and exposure of the cave fill was a late, not early Holocene event as previously assumed.

Two fractions of the Schuiling Cave human bone were prepared for ^{14}C analysis at the Radiocarbon Laboratory, University of California, Riverside. Since a preservative (Glyptal) had been applied to the bone, it was first necessary to extract the preservative with acetone and then remove the acetone under vacuum. Only about 1 gram of the bone was available for analysis. After removal of the surface matrix and acetone extraction, the amount of bone sample remaining was about 0.7 grams. Because of the minimum sample size and the degree of preservation of the organics, only a total organic and total inorganic (total carbonate) fraction could be isolated and the ^{14}C analysis carried out by accelerator mass spectrometry at the University of Arizona NSF Center for Radioisotope Analysis (Donahue et al. 1984).

The total inorganic fraction (UCR-1812A/AA-1874) of the Schuiling Cave human yielded an age of 12,100 $\pm$ 150 ^{14}C years B.P. The inorganic fraction of a bone typically reflects the degree of isotopic exchange with carbonates in the immediate vicinity of a bone sample rather than its actual age. That this process has apparently occurred is suggested by the ^{14}C age exhibited by carbonates in a soil sample collected from the middle portion of the cave profile where, as best could be ascertained based on the published description (Downs et al. 1959:16), most of the extinct vertebrate taxa found in the cave appeared to have been

collected. The apparent age of this soil $CaCO_3$ sample measured by conventional decay counting (UCR-2113) is 12,500 ± 150 ^{14}C years B.P.

By contrast, the ^{14}C age of the total organic fraction (UCR-1812B/AA-1875) is 3680 ± 200 ^{14}C years B.P. The ^{14}C age of an organic fraction in Holocene age bone typically reflects the actual age of the sample to within ±500–1000 years (Taylor and Slota 1979; Taylor 1982). It should be noted that the Schuiling Cave human bone contains significantly greater percentage amounts of four amino acids (aspartic acid, glutamic acid, glycine, and alanine) as compared with the percentage content of these same amino acids measured in a bone of an extinct species recovered from the middle levels of the Schuiling Cave deposit. The amino acid composition data is consistent with the ^{14}C results indicating the non-contemporaneity of the human bone and the Pleistocene fauna.

Regardless of the apparent stratigraphic association with extinct late Pleistocene vertebrate taxa, what appeared to be an identical degree of fossilization and an understanding of the depositional sedimentary context, the original assessment of the antiquity of LACM 47722 was in serious error. Estimated dates and apparent association based on similar criteria at other potentially early sites must always be carefully examined. Acceptance of a pre-Holocene age for any human remains in the Western Hemisphere whether recently excavated or discovered in existing collections, requires reliable laboratory analyses supported by adequate provenance and recovery data (Taylor et al. 1985).

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SOUTHERN CALIFORNIA ACADEMY OF SCIENCES ANNUAL MEETING

May 6 and 7, 1988

California State College at Northridge
Northridge, California 91330
Chairman: Larry Allen

Symposia planned to date: "Recruitment of Marine Fishes," "Biology of Cancer," "Tropical Biology," and "Structure and Change in Marine Communities in Southern California." Special sessions planned for "Topics in Geological Science" and on "Kelp Bed Ecology."

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Two Recent Occurrences of the Guadalupe Fur Seal *Arctocephalus townsendi* in Central California

In recent years, two Guadalupe fur seals, *Arctocephalus townsendi,* have beached along the central California coastline. On 25 April 1977 the first, a juvenile male, was found beached on the shore of Monterey Bay, near the southern boundary of Fort Ord, Monterey County; latitude 36°38′ north, longitude 121°50′ west. The second seal, a juvenile female, was found on 18 May 1984 in Princeton Harbor, San Mateo County; latitude 37°30′ north, longitude 122°29′ west (Fig. 1).

Once thought to be numerous from central Baja California to Point Conception, *A. townsendi* was all but exterminated by seal hunters by the close of the 19th century (Hubbs 1956). The occurrence of *A. townsendi* north of Point Conception is documented in two previous records. Three *A. townsendi* bulls were sighted at Piedras Blancas, San Luis Obispo County in 1938 (Bonnot et al. 1938), and Morejohn (1977) reported an *A. townsendi* humerus find in a pre-Spanish Indian habitation site between Elkhorn Slough and the city of Watsonville in Monterey County. Starks (1922) speculates that *A. townsendi* occurred as far north as the Farallon Islands off San Francisco. However, none of the skeletal material found thus far in sealer's middens on Southeast Farallon has been from *A. townsendi* (J. Schonewald, California Academy of Sciences, pers. comm.).

The species, now protected throughout its range, with a minimum population of 1600, breeds only on Guadalupe Island, Mexico (Peterson et al. 1968, Seagars 1984). It is regularly sighted on San Nicolas and San Miguel Islands off Southern California (Stewart 1981; Stewart et al. 1968). The seals described herein represent the northernmost 2 confirmed records of *A. townsendi.*

Both seals came ashore on sandy beaches, and were weak and emaciated when found. They were recovered by the California Marine Mammal Center (CMMC) for treatment and observation.

Upon arrival at CMMC, the juvenile male showed signs of moderate dehydration and slight congestion. He was nonaggressive, docile, quiet, and spent considerable time sitting with his head thrown back or lying prostrate, foreflippers drawn underneath or extended perpendicular to his body. During the second day, activity increased, and spells of diarrhea were noted.

He died suddenly in the early afternoon of his second day in captivity, 26 April. Post-mortem findings included a 2 cm by 4 cm erosive ulcer of the gastric mucosa, mild pneumonia, and an abscess of the upper left canine that led to necrosis. The latter caused degeneration of the ethmoturbinate of the left nasal passage and premature fusion of the maxillary suture above the left canine near the nasals. No traces of parasitism or food remnants were found. Weight at death was 6.2 kg.

The juvenile female was suspected to have been in Princeton Harbor at least three days prior to recovery by CMMC, and reportedly was being fed anchovies by local passersby. Once at CMMC, she was diagnosed as having a mild respiratory problem and bilateral cataracts causing impaired vision. Radiographs revealed a 20% pneumothorax of the left lung. She was lethargic but aggressive whenever handled.

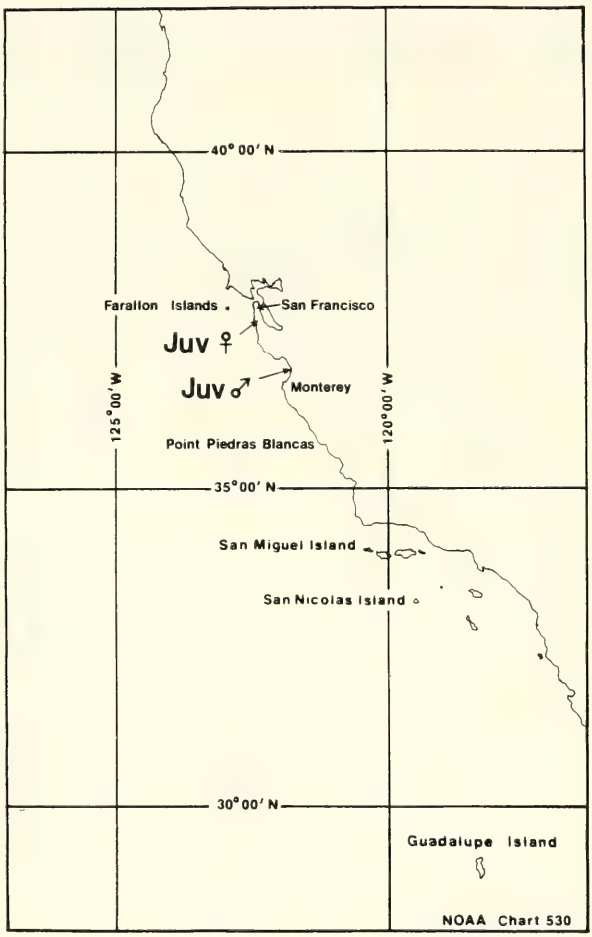

Fig. 1. Location of the occurrences of the juvenile male (CAS cat. # 20740) and juvenile female (CAS cat. # 22604) Guadalupe fur seals, *Arctocephalus townsendi* in central California.

Chloramphenicol, 150 mg, was administered prophylactively in her daily feedings. She was fed small (15–18 cm) Atlantic herring, *Clupea harengus,* three times a day. Initially, she was given 0.2 kg at each feeding, and later this was increased to 0.6 kg. Her weight more than doubled in the first six weeks at CMMC, from 6.8 kg to 14.5 kg. The first fecal sample from the juvenile female contained five otoliths, all from anchovy, *Engraulis mordax,* probably from the bait anchovy fed to her in Princeton Harbor. While in captivity at CMMC and Sea World, San Diego, she was maintained in a pen enclosure with access to a pool for grooming and exercise. The juvenile female died of anemia of unknown etiology on 30 November 1984 after 197 days in captivity.

The skeletons and skins of both seals are in the collections of the Department of Ornithology and Mammalogy, California Academy of Sciences (CAS). The juvenile male is CAS catalog number 20740; the juvenile female is CAS catalog

Table 1. External and skeletal characteristics used in the identification of the juvenile Guadalupe fur seals, *Arctocephalus townsendi.*

Identification characteristics	Citations
Narrow, upcurved muzzle with a bulbous terminal rhinarium.	Repenning et al. (1971)
Fur on dorsum of foreflippers extends over metacarpals.	Lyon (1937)
Upper postcanine toothrows diverge anteriorly and posteriorly.	Repenning et al. (1971)
Six upper postcanines.	Lyon (1937)
Three double-rooted upper postcanines.	Lyon (1937)
Diastema between the fourth and fifth upper postcanine.	Repenning et al. (1971)
Dental formulae: $\frac{3}{2}\cdot\frac{1}{1}\cdot\frac{6}{5}$	Repenning et al. (1971)
Angular process slopes medially to the body of the mandible at an angle of approximately 140°.	Lyon (1937)
Digastric prominence of the radius is present only as a slight rugosity.	Lyon (1937)
Pronounced pronator tres and slender proximal region between the head and proximal tres of the radius.	Lyon (1937)

number 22604. External and skeletal characteristics used in identification, and standard measurements (Scheffer 1967), are presented below (Tables 1 and 2, and Fig. 2). Based on the seasonal reproductive cycle of *A. townsendi* (Pierson 1978), size of the animals, characteristics of the skull, and comparison with known age *Callorhinus ursinus,* the juvenile male was estimated to be between nine and ten months old, and the juvenile female ten to eleven months old when found.

Acknowledgments

We wish to thank the following: J. S. Leatherwood, B. Stewart, R. L. DeLong, and W. Keener who reviewed the manuscript; J. Schonewald, S. Bailey, and L.

Table 2. Standard measurements of the juvenile male (CAS cat. #20740) and juvenile female (CAS cat. #22604) Guadalupe fur seals, *Arctocephalus townsendi.*

	CAS catalog number		
	20740 (death)	22604 (admission)	22604 (death)
1. Standard length (cm)	75	76	97*
2. Curvilinear (cm)	80	78	97.5*
3. Anterior length right foreflipper (cm)	25	28	31.5*
4. Anterior length right hind flipper (cm)	20.7	21	—
5. Axillary girth (cm)	—	51	66.5*
6. Weight (kg)	6.2	6.9	15.9*
7. Interorbital width (mm)	18	—	15
8. Zygomatic width (mm)	94	—	91
9. Cranial width (mm)	93	—	98
10. Condylobasal length (mm)	150	—	166
11. Basilar length of Hensel (mm)	135	—	149
12. Length upper left postcanine series (mm)	46	—	51

* Measurements taken on 21 October 1984, 40 days prior to death.

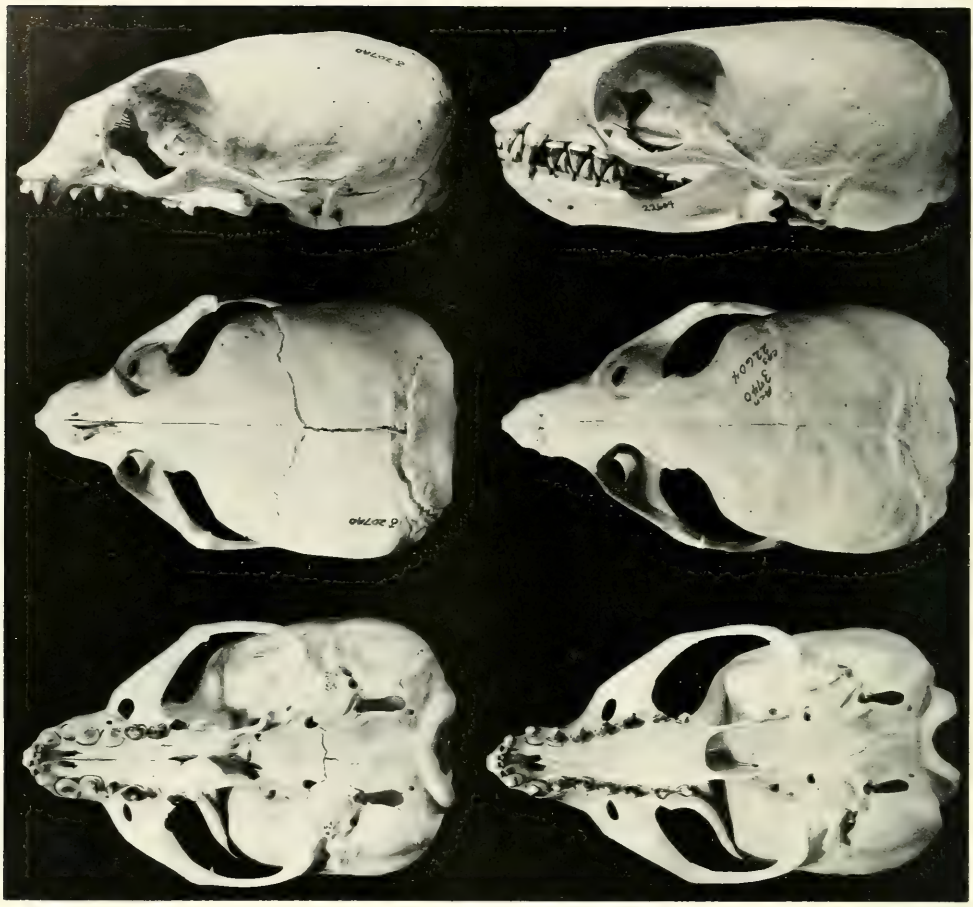

Figure 2. Lateral, dorsal, and ventral views of the Guadalupe fur seal, *Arctocephalus townsendi* skulls. Left: The juvenile male (CAS cat. # 20740). Right: The juvenile female (CAS cat. # 22604).

Thomsen for assistance at CAS; M. Lowry for identification of otoliths, C. A. Repenning for identification of the juvenile male; J. Patton and S. Middleton for the photographs; P. McKenzie for preparation of the map, and the animal caretakers and veterinary staff of the California Marine Mammal Center, and Sea World, San Diego.

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Seasonal Spawning Cycle of the Speckled Sanddab, *Citharichthys stigmaeus* (Bothidae)

The speckled sanddab, *Citharichthys stigmaeus* is one of the abundant marine flatfishes that occur in the coastal waters of southern California. It ranges from Magdalena Bay, Baja California to Montague Island, Alaska and is found at depths of 3–365 m (Miller and Lea 1976). There is little information on its reproductive biology. Ford (1965) reported spawning occurred April–September off southern California. The purpose of this note is to report on a histological analysis of females from seasonal collections.

Fish were collected by otter trawl off the coast of southern California at depths of 45–64 m from San Clemente (lat. 33°20′N, long. 117°38′W) to Huntington Beach (lat. 33°40′N, long. 118°00′W). Samples were from January 1978, February–April 1977, June–August 1977, September 1974, October–December 1977. Only females were examined. Specimens were immediately slit along the abdomen and placed in 10% formalin. Ovarian histological sections from 161 *C. stigmaeus* were cut at 8 μm and stained with Harris' hematoxylin followed by eosin counterstain. Seasonal gonosomatic indices (ovary wt/fish wt × 100) were calculated from preserved fish.

Ovaries were histologically classified into four stages (Table 1). Stage 1 (regressed or regressing ovary): the nonspawning condition consists mainly of primary oocytes (38 μm in diameter); Stage 2 (previtellogenic): slightly enlarged vacuolated oocytes (75 μm in diameter) predominate prior to onset of yolk deposition; Stage 3 (vitellogenic): yolk deposition in progress; Stage 4 (spawning): mature (ripe) oocytes (255 μm) and/or hydrated eggs (350 μm) predominate.

C. stigmaeus undergoes a spawning cycle in which spawning occurs March to October. During this period ovaries contain a mode of mature yolk-filled oocytes and/or hydrated eggs. In hydration, the oocyte may grow to as much as four times

Table 1. Monthly distribution of standard lengths and stages in *Citharichthys stigmaeus* spawning cycle.

Month	N	Range (mm)	Regressed (%)	Previtellogenic (%)	Vitellogenic (%)	Spawning (%)
January	18	73–105	83	0	11	6
February	1	84	0	0	0	100
March	18	56–86	0	0	6	94
April	10	54–80	0	10	30	60
June	18	65–89	0	0	12	88
July	18	64–87	0	0	0	100
August	18	73–95	0	0	0	100
September	16	62–86	0	0	0	100
October	18	78–93	17	0	0	83
November	3	68–76	100	0	0	0
December	4	71–90	50	0	0	50

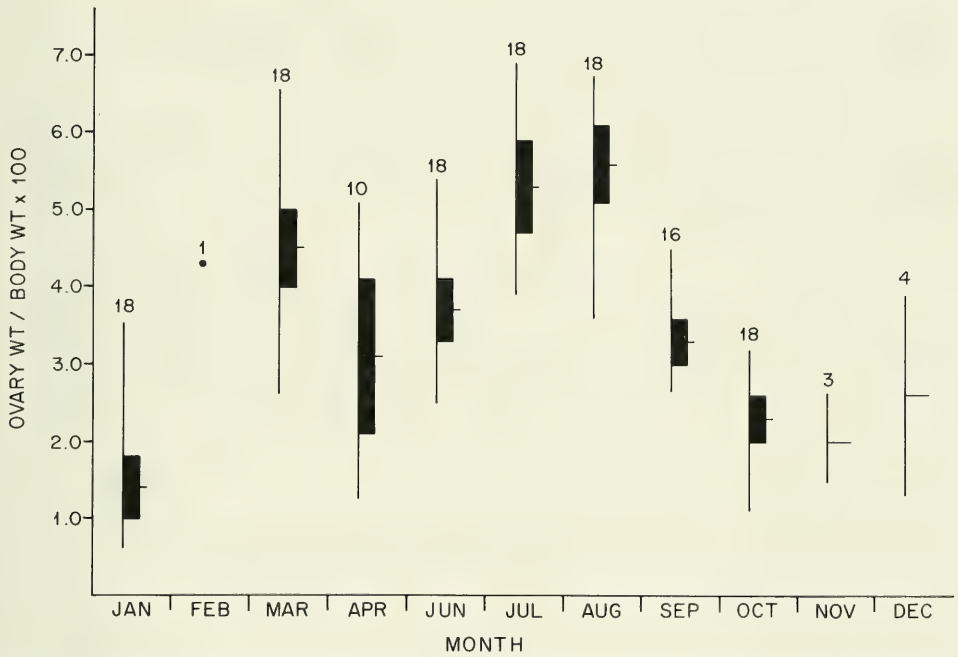

Fig. 1. Seasonal gonosomatic indices for *Citharichthys stigmaeus*. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval. Sample size above each month.

its original volume (Wallace and Selman 1981) making these structures readily identifiable. The presence in ovaries of mature and/or hydrated eggs (upcoming spawning) and vitellogenic eggs with yolk deposition in progress for a subsequent spawning indicate *C. stigmaeus* is a multiple spawning fish. The smallest fish in spawning condition measured 59 mm standard length.

There was a significant ($P < .05$) decrease in gonosomatic indices in autumn even though the majority of the population was in spawning condition. Our findings of March-October spawning contrast with Ford (1965) who found ripe females to occur during a shorter period (April–September). These observations may indicate year to year variation in duration of the spawning period. On the other hand, Ford's (1965) females were collected at shallower depths (5–30 m) than our samples. Consequently, these variations in duration of the spawning period may have resulted from exposure to different depth related water temperatures.

Our data have shown *C. stigmaeus* to have a prolonged spawning period that approximates eight months (March–October). This extended spawning period appears to be intermediate between the two types of spawning periods seen in California flatfishes. The first type is year-round spawning which occurs in two species. These fishes are *Pleuronichthys verticalis* in which spawning was described by Goldberg (1982a) and *Glyptocephalus zachirus* which Frey (1971) studied.

Other flatfish species, in contrast, have shorter spawning periods with a tendency toward winter spawning. Fitch and Lavenberg (1971) reported the following spawning periods: *Platichthys stellatus,* November–February; *Microstomus pacificus,* November–March; *Citharichthys sordidus,* July–September; *Paralichthys*

californicus, February–July. Goldberg (1981) reported summer spawning in *Symphurus atricauda* and summer–fall spawning (Goldberg 1982a) in *Hippoglossina stomata.* The majority of *Citharichthys xanthostigma* spawning occurs December–February in southern California (Goldberg 1982b).

With such a long period for spawning (eight months), *C. stigmaeus* females could presumably periodically refrain from spawning during unfavorable periods and still produce multiple batches of eggs each year.

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An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* accompany a *feature article. Abstract should not exceed 100 words.*

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Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54:452–458.

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COVER: Woodrat photograph by Kenneth P. Dial.