

Sand Crab Population Biology on the California Islands and Mainland

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Abstract - Population structures of sand crabs, *Emerita analoga*, living on Santa Catalina, Santa Cruz, Santa Rosa, and San Miguel Island beaches were compared to those for sand crabs inhabiting sites on the mainland coast of southern and central California. For the mainland sites, maximum male and female crab sizes, maximum and minimum ovigerous female crab sizes, and the size at maturity of female crabs increased significantly with coastline distance from south to north. Those same population measures for crabs from island sites showed the same trend from south to north over distance, but were more marked compared to the mainland sites. Water temperature was correlated inversely with the five population measures of crab size at both mainland and island sites and was a better predictor of crab measures than coastline distance for the island sites. Sand crab population characteristics were sensitive indicators of regional and inter-island differences in oceanographic conditions.

Introduction

The area near Point Conception generally is considered a transition zone (for discussion see Hayden & Dolan 1976; Horn & Allen 1978; Newman 1979; Doyle 1985) between the Oregonian and Californian marine biogeographic provinces on the West Coast of North America (Valentine 1966; see more extensive review by Brusca & Wallerstein 1979). The northern Channel Islands lie within or adjacent to this transition zone (see Fig. 1 in Seapy & Littler 1980). San Miguel and Santa Rosa Islands are at the northern edge, Santa Cruz Island is in the middle, and Anacapa

Island is at the southern edge. Santa Catalina, a southern Channel Island, lies well south of the transition zone.

Previous workers (Cockerell 1938; Hewatt 1946; Murray *et al.* 1980; Seapy & Littler 1980; Murray & Littler 1981; Engle 1993) recognized the north-south mixture of flora and fauna on the Channel Islands in their studies of species diversity. In studies of marine invertebrates on Santa Cruz Island, Cockerell and Hewatt designated species as either "northern" or "southern" forms, on the basis of whether they were normally found either north or south of Point Conception.

In Hewatt's study, Santa Cruz Island had nearly equal representation from both northern and southern faunal provinces, as well as some species which occur along the entire California coastline. Seapy & Littler (1980) and Murray & Littler (1981) found notable differences between intertidal faunal assemblages, even at times on the same island. Murray & co-authors (1980) reported similar results for algal species on the islands. Engle (1993) found similar patterns in fish diversity. Patterns of biological variation within a single species across broad geographic ranges on the west coast of North America have revealed gradients in size, growth, and survival (*e.g.*, Weymouth *et al.* 1931; Frank 1975; Hines 1989; Dugan 1990; Dugan *et al.* 1991). However, with the exception of McGill's 1979 study of genetics in *Ligia occidentalis*, few investigators have compared the variation found in the biology of a single intertidal species inhabiting both the California Islands and the mainland.

Sand crabs (*Emerita analoga*) are a particularly appropriate organism for a comparative study of geographic variation in biology (Wenner 1987). This species occurs on exposed sandy

beaches from Vancouver Island, Canada, to Magdalena Bay, Baja California, Mexico (Efford 1969, 1970) and spans the transition zone noted above. As larvae, sand crabs spend at least two and a half months in the plankton before settling as megalopa on beaches (Johnson & Lewis 1942; Barnes & Wenner 1968; Efford 1970). That time in the ocean allows for extensive planktonic dispersal and mixing (Johnson 1940); for example, Beckwitt (1985) found no large scale genetic trends among sand crab populations in central and southern California.

Once sand crabs have settled on a beach, movement is restricted to tidal migration and the

relatively short distance that longshore transport may carry them. Post-settlement transport of juvenile and adult populations between islands or between islands and mainland is not possible during their adult life span of 2-3 yr. The dynamic distribution of sand crabs on a beach also allows geographic comparisons to be made without tidal height corrections.

In addition, sand crabs filter feed with their plumose second antennae, straining plankton from the water; their diet appears to consist mainly of phytoplankton (Efford 1966; Barnett 1984). As in most decapod crustaceans, eggs are brooded externally, permitting ready assessment of reproductive condition.

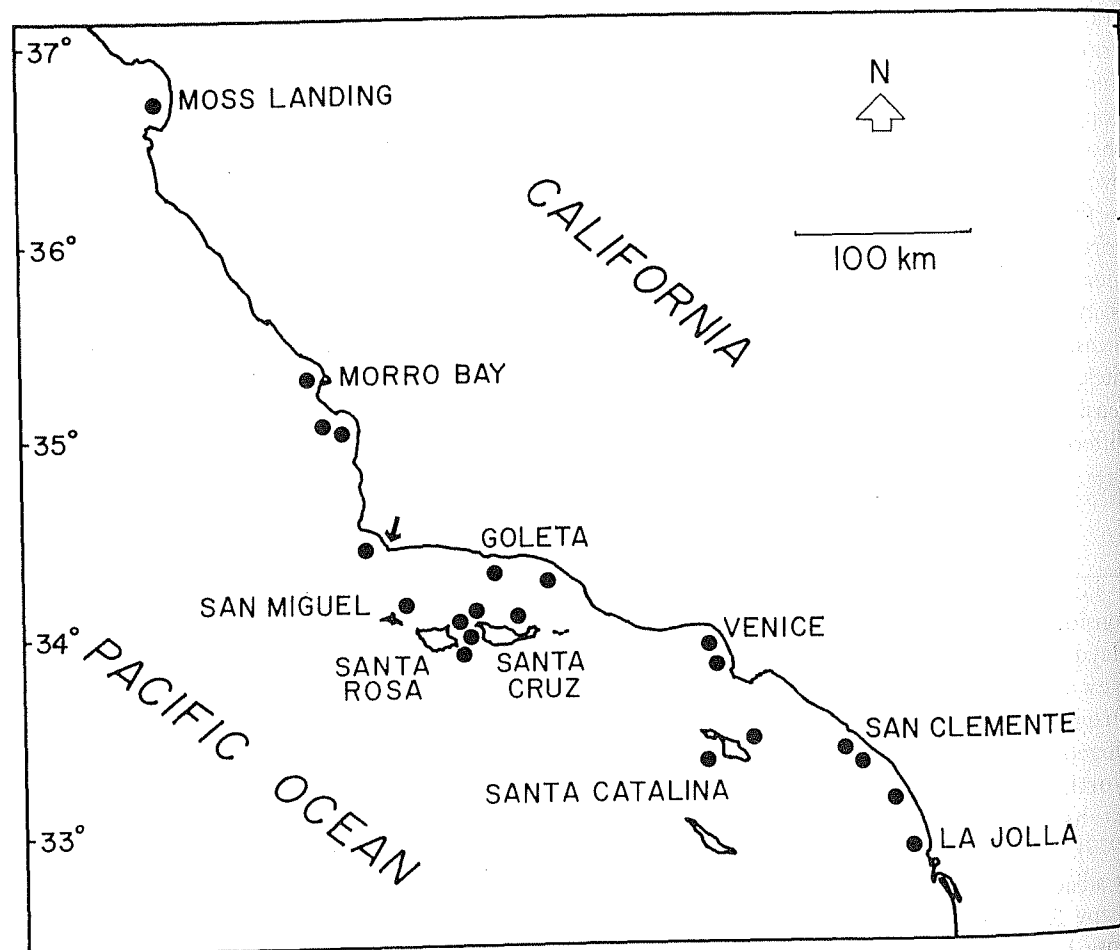


Figure 1. Map of study sites along the central and southern California coastline. The arrow designates the location of Point Conception.

Our study compared sand crab reproduction and population structure of samples obtained at eight sites on four of the California Islands (Santa Catalina, Santa Cruz, Santa Rosa and San Miguel) with samples obtained from 14 sites on the mainland, ranging from Moss Landing to La Jolla, California.

Methods

Sand crabs (*Emerita analoga*) were collected at eight sites on four of the California Islands and at 14 mainland sites (Fig. 1). Crabs were collected and measured to the nearest 0.5 mm or 1.0 mm carapace length (CL), after the method of Wenner & co-authors (1974) and Siegel & Wenner (1984). In all cases we

attempted to get a full spectrum of crab sizes, but we did not sample for density or abundance (see Wenner 1987). The 4-wk sampling period ran from 25 July to 26 August 1986, the height of the reproductive season (Wenner *et al.* 1985); samples also were taken at some sites during the same period in 1984 and 1985. Sampling sand crab populations from many sites during a short time span provided data with a minimum influence of seasonal variation on the size measures under consideration (Wenner *et al.* 1985). Sea water temperature was measured in the wash zone at the time of each sample.

We used five measures for comparisons (Wenner & Fusaro 1979; Wenner 1987), as follows: 1) maximum size of male crabs, defined

Table 1. Sampling sites, dates, coastline distances, temperatures at the time of collection, sample size and five population parameters (mm CL) for *Emerita analoga* populations from mainland and island beaches in 1986.

Sampling Sites	Date	Distance (km)	Temp. (°C)	Sample Size	Maximum Male Size	Maximum Female Size	Minimum Ovigerous Female Size	Mean Minimum Size	Maximum Ovigerous Female Size
MAINLAND									
Moss Landing	8/10	0	14	1503	12.0	21.9	16.7	18.8	32.8
Morro Bay	8/13	163	14	552	13.1	22.9	18.8	16.2	22.9
Avila Beach	8/13	186	16	1268	11.0	24.0	16.2	16.7	24.0
Pismo Beach	8/13	192	16	1861	11.0	19.8	15.1	18.8	19.8
Jalama	7/25	244	16	1365	9.9	20.9	14.1	13.1	20.9
Pt. Conception		252							
Goleta	8/4	296	20	755	9.4	19.8	11.5	12.0	19.8
Sea Cliff	8/4	335	16	1457	9.4	19.8	13.1	13.1	19.8
Venice	8/12	427	20	1647	9.9	16.7	12.0	12.0	16.7
Hermosa Beach	8/12	441	21	3017	10.5	16.2	12.0	13.1	16.2
San Clemente	8/15	530	17	1178	9.4	18.8	11.5	10.5	18.8
San Onofre	8/15	537	19	548	7.9	11.5	9.4	9.9	12.0
Oceanside	8/15	560	18	841	9.9	21.9	12.0	12.0	21.9
Solana Beach	8/17	589	19	2025	8.9	13.6	9.9	9.9	13.6
La Jolla	8/17	597	18	1468	9.4	16.2	11.5	10.5	16.7
ISLAND									
San Miguel Island									
Cuyler's Harbor	8/20	276	13	1816	12.8	18.8	13.1	16.7	26.1
Santa Rosa Island									
Beecher's Bay	7/31	307	16	680	11.0	22.9	12.0	14.9	24.0
Water Canyon	7/31	310	18	625	11.0	22.9	13.1	15.1	27.6
Santa Cruz Island									
Forney Cove	8/5	318	17	1927	8.4	11.0	9.9	14.1	18.0
Christi Beach	8/5	321	18	3031	7.3	11.0	9.9	11.5	18.8
Prisoner's Harbor	8/7	338	18	227	7.3	11.5	7.9	9.4	12.0
Santa Catalina Island									
Little Harbor	8/26	470	20	607	7.3	9.4	8.9	7.9	11.5
White's Landing	8/26	477	21	429	6.8	11.0	7.3	---	9.4

as the size of the 95th percentile male in the sample taken; 2) maximum size of female crabs (size of the 95th percentile female with or without eggs); 3) minimum size of ovigerous female crabs (size of the 5th percentile ovigerous female); 4) female size at maturity, as defined in Wenner & co-authors (1974, 1985) and Dugan & co-authors (1991) and 5) maximum size of ovigerous female crabs (size of the 95th percentile ovigerous female crab). Use of the 5th and 95th percentile levels minimized the influence of extreme values.

Coastline distances for each site were measured from Moss Landing and along a baseline running through Pismo Beach and La Jolla (Table 1). Data from San Onofre were not included in figures or in statistical analyses due to the anomalous reproduction and population structure found there (Siegel & Wenner 1984).

Results

Significant north to south trends were found in all five population parameters for island and mainland sites (Table 1) (Spearman's rank correlation test: $P < 0.01$). Sand crabs both matured at and attained larger sizes at mainland sites north of Point Conception and at sites on San Miguel and Santa Rosa Islands than at mainland sites in the Southern California Bight or at sites on Santa Cruz and Santa Catalina Islands. Sea water temperatures increased significantly from north to south (Spearman's test: $P < 0.005$). Table 1 contains a summary of results found for the five characteristics measured in sand crab populations inhabiting island and mainland sites.

A Comparison of Two Island and Two Mainland Sites: Comparisons of the overall population structure of sand crabs for two of the island sites and two of the mainland sites (Fig. 2) illustrate the north to south trends found. The population structures of sand crabs at these four sites exhibited similar characteristic patterns but very different size ranges of crabs. A polymodal size structure prevailed at most of the sites (Wenner *et al.*

1987a), with at least two year classes for female crabs evident as 2-3 size modes as illustrated for Avila, San Miguel Island and San Clemente State Beach (Figs. 2A, 2B, and 2C). The sand crab data from Santa Catalina Island formed a unique unimodal size distribution (Fig. 2D).

Small crabs (<10 mm CL) occurred at all sites (as illustrated for the 4 sites in Fig. 2). That pattern is consistent with recruitment of sand crab megalopa during the spring of 1986. Female crabs attained much larger sizes than males (see Wenner & Haley 1981) at all sites, as illustrated for the four sites in Figure 2. The sizes of the largest female sand crabs were approximately 30 mm CL at San Miguel Island and Avila Beach (Figs. 2A, 2B), 22 mm CL at San Clemente State Beach (Fig. 2C), and 11 mm at Santa Catalina Island (Fig. 2D). Overall, the largest maximum size of female crabs occurred at Moss Landing (32.8 mm); the smallest maximum size was found at Santa Catalina Island (9.4 mm).

Size ranges of ovigerous female crabs did not overlap in samples from San Miguel and Santa Catalina Islands (Figs. 2B, 2D). Overlap in size ranges of ovigerous females did occur in data from the mainland, Avila Beach and San Clemente State Beach (Figs. 2A, 2C), but crabs at Avila Beach reached much larger sizes than the others in that comparison. Populations at San Miguel Island and Avila had similar size ranges of ovigerous female crabs (Figs. 2A and 2B), as well as similar maximum sizes of male and female crabs. However, female crabs matured at a smaller size on San Miguel Island than at Avila. The smallest size at maturity for all sites occurred at Santa Catalina Island (Fig. 2D).

Sand crabs from the San Miguel Island site (Fig. 2B) reached much larger sizes in all five measures than crabs on Santa Catalina Island (Fig. 2D). However, crabs from San Miguel Island (Fig. 2B) attained only slightly smaller maximum sizes, on the whole, than those collected at the Avila site (Fig. 2A), 194 km to the north. The range of variation in sand crab sizes at those two island sites (Figs. 2B, 2D) was more different than that found between the

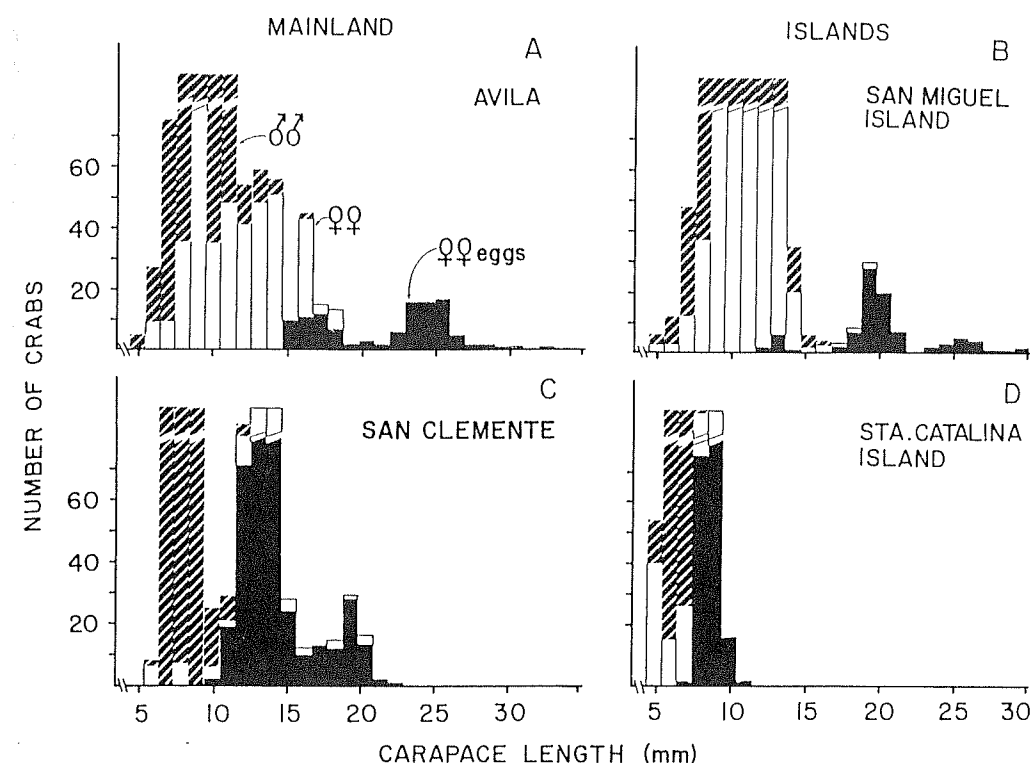


Figure 2. Size frequency distributions of sand crab population samples at two island sites and two mainland sites.

two mainland sites (Figs. 2A and 2C) or between the San Miguel Island and Avila mainland sites.

Maximum Sizes of Crabs: The comparisons shown in Figure 2 reflect trends for the survey as a whole. Maximum sizes attained by male and female crabs decreased significantly (Spearman's test; $P < 0.01$) from north to south for both island and mainland sites (Table 1). The differences found in maximum male crab size were nearly twofold at the island sites but somewhat less between mainland sites. The maximum size of female crabs varied by more than a factor of two at the island sites but showed a smaller range of variation at mainland sites.

In general, the largest male and female sand crabs from the San Miguel Island and Santa Rosa Island sites were similar in size to the largest crabs found north of Point Conception (Table 1). The largest crabs collected on the

northeastern side of Santa Cruz Island and on Santa Catalina Island were smaller in size than any of the maximum-sized individuals found on mainland beaches in the Southern California Bight.

Sizes of Ovigerous Crabs: The sizes of ovigerous crabs varied greatly at the sites sampled. The largest amount of variation present in any population measure occurred in the maximum size of ovigerous crabs at the different localities; nearly a three to one difference existed, from north to south, at both island and mainland sites. The size of the smallest ovigerous crabs and the size at maturity of female crabs varied somewhat less on the islands than on the mainland.

The size at maturity of female crabs decreased significantly (Spearman's test; $P < 0.001$) with coastline distance from north to south, both along the mainland coast and along the island chain (Fig. 3). A significant decrease

from north to south also occurred in the other two measures of ovigerous crab size (Spearman's test; $P < 0.001$). The decrease from north to south for the island sites was much steeper for size at maturity and other reproductive measures than it was for the mainland sites (Fig. 3).

Temperature Correlations: All five population parameters were negatively correlated with surf zone water temperatures at the time of collection ($P < 0.01$) (Table 2). When the size at maturity of female crabs was examined as a function of temperature (Fig. 4), the striking contrast found between the island and mainland data in relationship to coastline distance (Fig. 3) was no longer evident. For both island and mainland sites, larger maximum sizes of male and female crabs were found at sites bathed by colder waters, while smaller maximum sizes of individuals of both sexes were found at warmer water sites.

Between Years Variation: The patterns of variation found in sand crab populations between island sites in 1986 generally matched the patterns we found in 1984 and 1985. The comparison of the sizes of largest ovigerous female crabs given in Table 3 illustrates that point. Results from the two mainland sites shown in Table 3 are presented for comparison.

The values shown for the 1984 data were generally smaller than the values found in 1985. The 1984 survey followed one of the most pronounced El Niño events on record (Fiedler 1984) for California waters. The following year, 1985, was the first year after that event in which colder water temperatures existed near the islands.

Discussion

The variation found in the reproduction and population structure of sand crabs (*Emerita analoga*) inhabiting island and mainland beaches far exceeded any differences one might expect for such apparently similar habitats. Some of the smallest maximum sizes of reproductive sand

crabs ever found in our extensive sampling program along the California coastline were found at Santa Catalina Island. On the other hand, the maximum size of sand crabs from San Miguel Island beaches were nearly as large as those found anywhere else in California.

Previous Studies of Sand Crab Population Structure: Sand crabs of various species (Family Hippidae) have proved to be especially suitable animals for studies of variation in population structure as a function of geographic location (Osorio *et al.* 1967; Efford 1969, 1970; Fusaro 1977, 1978; Auyong 1981; Dugan & Wenner 1985; Wenner 1987; Wenner *et al.* 1987b; Dugan 1990; Dugan *et al.* 1991). Efford (1969, 1970) found no geographic trends in sand crab (*Emerita analoga*) population structure along the West Coast. However, he did not collect crabs from the California Islands, and his data were collected at different times of the year and in different years.

A comparison of the results of Cox & Dudley (1968) at La Jolla and Eickstaedt (1969) at Monterey indicates that sand crabs in the Monterey Bay area were considerably larger than those in the La Jolla area. Studies of growth rate and population structure of sand crabs on Santa Cruz Island and at Goleta, California (Fusaro 1977, 1978) revealed that crabs grew slower and reached smaller maximum sizes at that island site than at the mainland site. He attributed the differences in growth and size to the effect of colder waters and lower food levels at the island site. Auyong (1981) studied sand crab populations at beaches only in the southern portion of the Southern California Bight.

Dugan & Wenner (1985), Wenner & co-authors (1987a), Dugan (1990), and Dugan & co-authors (1991) reported significant geographic variation in egg numbers and sizes of reproduction for sand crab populations on the California coast, particularly for those populations living north versus south of Point Conception. Crabs in the north matured at and

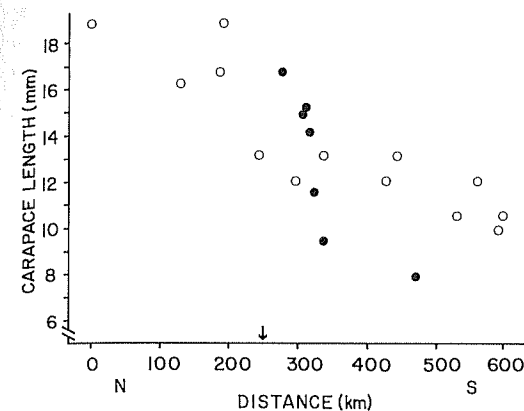


Figure 3. Mean size at onset of egg production as a function of coastal distance from Moss Landing, Monterey County. Open and closed circles represent mainland and island sites, respectively.

attained larger sizes than those south of Point Conception, due to higher growth rates in the north (Dugan & Wenner 1985).

Variation in Sand Crab Population Structure in This Study: This present study began with the 1983 finding (Wenner, unpubl. data) that reproduction and size ranges were remarkably different for sand crabs living on beaches only 10 km apart on Santa Rosa and Santa Cruz Islands (see Table 3). The five sand

Table 2. Correlations and least square regressions obtained between surf zone water temperatures ($^{\circ}\text{C}$) at the time of collection and the five population parameters for *Emerita analoga* samples (Significance levels: ** = $P < 0.01$; *** = $P < 0.001$).

Parameter (mm CL)	Regression (y)	Correlation Coefficient (r)	Sample Size (n)
Maximum size male crab	$-0.57x + 19.6$	0.68***	22
Maximum size female crab	$-1.27x + 39.5$	-0.57**	22
Minimum size ovigerous crab	$-0.93x + 28.4$	-0.70***	22
Female size at maturity	$-1.08x + 31.8$	-0.72***	21
Maximum size ovigerous crab	$-2.09x + 56.5$	-0.73***	22

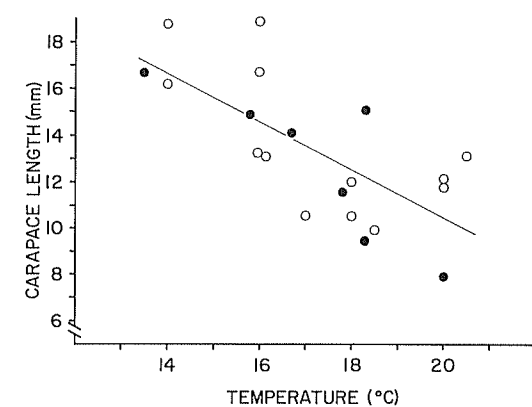


Figure 4. Mean size at onset of egg production as a function of temperature at the time of collection (symbols as in Fig 3).

crab variables relating to size, as measured in this study, revealed significant decreasing trends with coastline distance, from north to south, both on the islands and on the mainland. Those results correspond with the great differences obtained in the earlier studies of Cox & Dudley (1968) and Eickstaedt (1969) and with recent comprehensive studies of geographic patterns along the mainland coastline ((Dugan & Wenner 1985; Wenner *et al.* 1987a; Dugan 1990; Dugan *et al.* 1991).

Table 3. Maximum size ovigerous female *Emerita analoga* (size of 95%-ile individual, mm CL) in three successive years at eight island and two mainland sites.

Sampling Sites	1984	1985	1986
MAINLAND			
Avila Beach	28.1	29.2	24.0
San Clemente	13.0	15.7	18.8
ISLAND			
San Miguel Island			
Cuyler's Harbor			26.1
Santa Rosa Island			
Beecher's Bay	25.0	26.1	24.0
Water Canyon	24.5	26.1	27.6
Santa Cruz Island			
Forney Cove	15.1	20.9	18.0
Christi Beach	14.4	18.8	18.8
Prisoner's Harbor		13.1	12.0
Santa Catalina Island			
Little Harbor			11.5
White's Landing			9.4

Population structures and reproduction of sand crabs living on the California Island beaches were often strikingly different from those of sand crabs inhabiting directly opposing mainland or (in some cases) other island beaches. Sand crab populations sampled on San Miguel and Santa Rosa Islands, for example, were more similar to populations living north of Point Conception than to those living on nearby Santa Cruz Island beaches (only 10 km distant).

Populations on Santa Cruz Island were more similar to those sampled at mainland and island beaches far to the south than they were to populations inhabiting beaches directly to the north on the mainland (e.g., Goleta in Table 1). Sand crab populations at beaches on the northeastern side of Santa Cruz Island were more similar to Santa Catalina Island beaches than they were to beaches on the western half of Santa Cruz Island.

Polymodality was evident in the size distributions; first and second year classes (Siegel & Wenner 1985; Wenner *et al.* 1987a) appeared to be present in the mainland Avila, San Miguel Island and mainland San Clemente populations (Figs. 2A, 2B, 2C), as well as at most other sites represented in Table 1. However, the unimodal population structure obtained from two beaches at Santa Catalina Island (Fig. 2D) appeared to be composed of only first year crabs. The apparent absence of older overwintered crabs there could represent a failure at overwintering, perhaps as a consequence of insufficient food, selective predation, isolated larval recruitment, or physical factors (Wenner 1987).

The range of values for measures of population structure in sand crabs along the length of the California Islands archipelago in the Southern California Bight was similar to that observed over a much greater distance on the California mainland coastline in this and in other studies (Dugan 1990; Dugan *et al.* 1991). The intraspecific geographic trends in population structure of sand crabs and the apparent lack of genetic trends over the range

of the study (Beckwitt 1984) indicate that this species adapts to a wide range of environmental conditions.

Geographic Variation in Other Species:

In general, intraspecific comparisons of individual size have revealed larger sizes at higher latitudes than at lower latitudes within crustacean species (see Abele 1982) and for other marine invertebrates (Newell 1964; Frank 1975) over a broad geographic range. Studies include: 1) measures of variation in size at maturity (Annala *et al.* 1980: lobster, *Jasus edwardsii*; Jones & Simons 1983: crab, *Helice crassa*; Hines 1989: brachyuran crabs); 2) variation in overall sizes (Frank 1975: snail, *Tegula funebris*; Weymouth *et al.* 1931: clam, *Siliqua patula*; Fawcett 1979: *T. funebris*; Jones & Simons 1983: *Helice crassa*) and 3) differences in growth rates (Weymouth *et al.* 1931: *S. patula*; Frank 1975: *T. funebris*).

Other studies have involved comparisons of population variation between only two or at most a few sites. They include: 1) size at maturity (Smith & Breyer 1983: snail, *Epitonium tinctorum*); 2) overall size differences (Schmidt 1993: periwinkle, *Littorina keenae*; Willason *et al.* 1986: copepod, *Calanus pacifica*); 3) differences in population structure (Smith & Breyer 1983: *E. tinctorum*; Schmidt 1993: *L. keenae*; Cox *et al.* 1983: *C. pacifica*) and 4) variation in brooding activity with location (Cimberg 1981: gooseneck barnacle, *Pollicipes polymerus*). On a related matter, McGill (1979) found genetic variation and variation in shape, size and egg number for the intertidal isopod *Ligia occidentalis* in populations on the islands and mainland.

Oceanographic Patterns and Processes:

Temperature directly or indirectly affects both the biology and distribution of marine organisms (Fusaro 1980: *Emerita analoga*; see Brusca & Wallerstein 1979 for discussion). The differences found in sand crab reproduction and population structure in this study may be related to the spatial and temporal patterns of water temperature (Fig. 5) and food supply (e.g., plankton) in coastal waters.

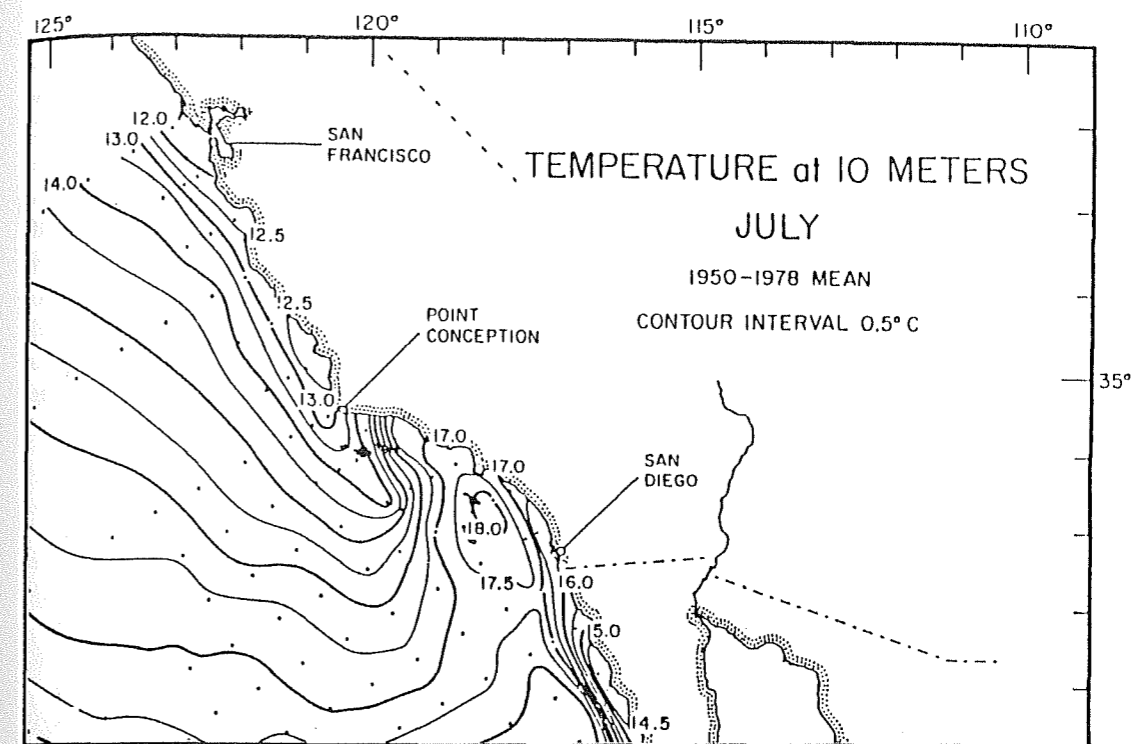


Figure 5. A 28 yr average of July water temperature at 10 m along the central and southern California coast. A plume of cold water from the upwelling region north of Point Conception bathes San Miguel, Santa Rosa and San Nicolas Islands. (Adapted from Lynn *et al.* 1982:347).

The temperature, nutrient, phytoplankton and zooplankton composition of water masses along the California coast is complex. The north to south increase in water temperature is not uniform; an abrupt change usually occurs just south of Point Conception (Fig. 5). The flow of the California Current (Reid *et al.* 1958) moves sub-arctic waters to the south. Wind driven coastal upwelling can bring nutrient rich cold water to the surface, particularly between Cape Mendocino and Point Conception during spring and summer (Bakun *et al.* 1974).

Cool and relatively nutrient rich water may extend south beyond Point Conception as a plume (Reid *et al.* 1958) or as a series of eddies (Lasker *et al.* 1981). That water mass may become further augmented by other mixing and upwelling south to the Cortez Bank (Owen 1980). Winds, currents, and the orientation of various headlands, islands, and

banks contribute to those processes (Reid 1965; Pelaez & Guan 1982), along with advection in cyclonic eddies such as the Southern California Eddy (Owen 1980). Eckman pumping driven by wind stress curl (Chelton 1982) may augment the cool rich water plume or eddies.

Water temperature patterns in the Southern California Bight are a consequence of the above influences. Long-term averages for July (Lynn *et al.* 1982:347) show the extension of cool waters into the northwestern portion of that bight (Fig. 5), which includes San Miguel and Santa Rosa Islands. A steep west-east gradient occurs in the northern Channel Islands region, particularly in the vicinity of Santa Cruz Island. Intermediate water temperatures are found along the mainland coast and the warmest waters occur in the southern portion of the Bight (including Santa Catalina and San Clemente Islands).

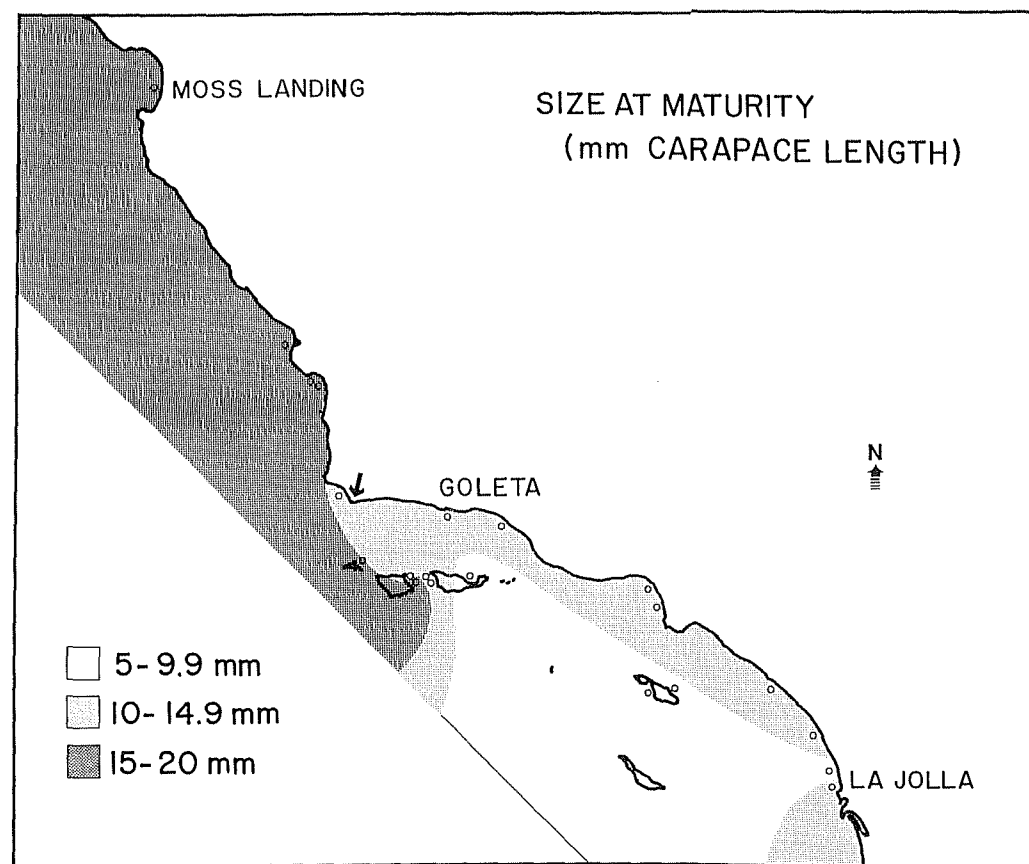


Figure 6. Patterns in size at onset of egg production along the central and southern California coastline.

Infrared and chlorophyll satellite imagery of waters off southern and central California in spring and summer reveal regional patterns consistent with long-term temperature averages (see Fig. 6 in Pelaez & Guan 1982; Fiedler 1984). Satellite imagery also provides information on short term and relatively small scale variation, often revealing a band of high chlorophyll levels adjacent to the mainland coast (Pelaez & Guan 1982; Smith & Baker 1982; Fiedler 1984).

The correlations obtained in this study seemed to implicate temperature as a factor in the significant variability found in sand crab

reproduction and population structure, in that the data on sand crab biology (Fig. 6) matched the temperature profile present in summer months (Fig. 5). However, since other entities may co-vary with temperature in this region, those correlations could also reflect the availability of nutrients (Thomas & Siebert 1974) and phytoplankton (Owen 1974) in water masses associated with the California Current, its eddies, and the Southern California Countercurrent.

Biogeographic Implications: The intraspecific geographic variation observed in the population biology of *Emerita analoga*

inhabiting the California Islands was in agreement with patterns found in earlier studies of species diversity among the islands: 1) marine algae (Neushul *et al.* 1967; Murray, *et al.* 1980; Murray & Littler 1981); 2) seabirds (Hunt *et al.* 1980); 3) pinnipeds (Le Boeuf & Bonnell 1980); 4) sandy beaches (Straughn & Hadley 1980); 5) rocky intertidal systems (Littler 1980); 6) rocky intertidal invertebrates (Seapy & Littler 1980) and 7) mussel communities (Kanter 1980). Hunt & co-authors (1980) summed up a common finding in those diversity studies, as follows:

"...the Channel Islands provide a meeting ground for northern and southern species of various diverse faunal groups. Forms that typically occur north of the [Southern California] Bight occur most commonly at the west end of the northern chain of islands, while the east end of the northern chain and the southern islands show a predominance of species with southern affinities."

The results we obtained in studies of reproduction and population structure of sand crabs parallel that summary statement to some extent. Sand crab populations along the California Islands archipelago exhibited the same range of variation one finds along the mainland coast, but within a much shorter range of latitude. The abrupt change in the population biology of sand crabs on the islands occurred at the gap between Santa Cruz Island and Santa Rosa Island; that gap, in turn, corresponded with the Point Conception faunal break on the mainland and with water masses bathing the islands.

Conclusion

In the present study, intraspecific comparisons of sand crab (*Emerita analoga*) populations at one time of the year revealed trends of increasing individual size and size at maturity for crabs from south to north along

the California coast. Populations of crabs on the two northwesternmost Channel Islands (San Miguel and Santa Rosa Islands) were more similar in size and size at maturity to sand crabs inhabiting mainland beaches located north of Point Conception than they were to the adjacent mainland coast. Crabs inhabiting the more southern islands (Santa Cruz and Santa Catalina Islands) were more similar to crabs inhabiting mainland beaches located well south of Point Conception. The reproduction and population structures of sand crab populations inhabiting mainland and island beaches reflected variation in the temperature and productivity of the water masses surrounding the islands.

Acknowledgments

We thank A. and R. Vail (Vail and Vickers Company, Santa Rosa Island), the late C. Stanton (Santa Cruz Island Company), L. Laughrin (University of California, Santa Cruz Island Reserve), T. Martin (Santa Catalina Conservancy), and F. Ugolini and D. Richards (National Park Service, San Miguel Island) for their support of our research and access to the California Islands. We also thank J. Stowe and A. Oliver for access to California State Parks, and D. Forcucci, P. Givens, B. Hanley, A. Harris, C. McNeil, M. Rajala, T. Stevens and K. Vines for their assistance with field work. M. Page critically reviewed the manuscript. The study was supported in part by a grant from the CS Fund.

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