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Geographic variation in life history of the sand crab, *Emerita analoga* (Stimpson) on the California coast: Relationships to environmental variables

Jenifer E. Dugan*, David M. Hubbard, Adrian M. Wenner

Marine Science Institute. University of California, Santa Barbara, CA 93106. USA

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Abstract

Geographic variation and the influence of environmental factors on life history characteristics of populations of a sandy intertidal decapod. *Emerita analoga*, Stimpson, inhabiting beaches along 8 ° of latitude on the California coast in midsummer were investigated for 5 yr. Female size at maturity, largest and smallest ovigerous crab size, and largest male crab size. expressed as carapace lengths, increased from south to north and were 1.5 to 3 times greater in northern than in southern populations. The observed trends in life history were associated with environmental factors that varied on regional (water temperature) and local scales (food availability and physical characteristics related to beach morphodynamics) using simple and multiple linear regression analyses. Incorporating regionally and locally varying environmental factors into a multiple linear regression model provided a better predictor of life history characteristics than any single factor. In every year, the four life history characteristics were negatively correlated with surf zone water temperature, which varied regionally and was correlated with coastline distance. Female size at maturity and the largest and smallest ovigerous crab sizes were positively correlated with food availability. estimated by chlorophyll *a* concentration. which was not correlated with coastline distance. Life history. characteristics were not correlated with any of the beach morphodynamic variables in simple regressions. Removal of variation associated with water temperature and chlorophyll *a* in multiple linear regression analyses yielded positive correlations between the sizes of the largest and smallest ovigerous crabs and the size of the largest male crab. and a beach characteristic. an index of sediment size and sorting. which was not correlated with coastline distance. Female size at maturity, largest and smallest ovigerous crab sizes and largest male crab size were correlated in each year. implying that these life history traits are influenced by similar mechanisms. Little interannual variation occurred in the geographic patterns observed in life history traits. Life history, traits examined in our study were correlated between years,

* Corresponding author

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suggesting that interactions between settlement, growth, survival, and environmental variables were relatively consistent during our study.

Keywords: Decapod; Life history; Sand beach

1. Introduction

Life history characteristics of marine organisms may be influenced by a variety of biotic and abiotic factors including: predation, competition. parasitism. genetic stock. water temperature, food availability, and wave exposure (Annala et al.. 1980; Wallerstein and Brusca, 1982: O'Brien. 1983; Page, 1984; Davidson et al.. 1985: Etter. 1989). Those factors may vary along geographic gradients or on local or temporal scales and result in geographic. local. and/or temporal variation in life history. Invertebrates inhabiting colder water and higher latitudes are predicted to mature at and attain larger sizes (Templeman, 1936; Abele, 1982; and Bergmann's rule *sensu* Mayr. 1942; Ray. 1960). Patterns fitting those predictions have been documented in studies of sufficient geographic scope in a variety of marine mollusks and crustaceans (Weymouth et al., 193 1; Hall and Hessler, 1971; Frank, 1975; Annala et al., 1980: Jones & Simons, 1983; Hines, 1989; Dugan et al., 1991). Local scale variation in life history has also been documented in some marine invertebrate species (e.g. Page, 1986; Etter. 1989; Bertness et al., 1991). Interannual variation in life history has rarely been addressed on local or regional scales.

Open coast sand beaches are one of the most dynamic and harsh marine intertidal environments (McLachlan et al., 1993). It is generally believed that sand beach macrofauna communities are structured more by independent responses of populations to physical factors than by biological interactions between species and individuals (McLachlan, 1983, 1990). Geographic patterns in sand beach community structure are not well described. Species diversity, zonation, distribution, abundance. and total biomass of beach macrofauna communities and the population distribution and abundance of macrofauna species have been correlated with physical characteristics of sand beaches that vary on local scales including: sediment grain size, wave exposure. beach slope, sand moisture content, Dean's parameter, swash climate. and food availability (Eleftheriou & Nicholson, 1975; McLachlan et al.. 198 1, 1993; McLachlan, 1983, 1990; McLachlan & Hesp, 1984: Sastre, 1984; Bowman & Dolan, 1985; Shepherd et al.. 1988; Fleischack & Freitas. 1989; McArdle & McLachlan. 1991). Given the importance of physical processes in structuring exposed sand beach communities, the life history of sand beach macrofauna species may vary predictably with the physical characteristics of sand beaches. Relationships between life history traits of populations of macrofauna and physical characteristics of beaches have not been investigated despite the evidence for local physical control of community structure and population distribution and abundance on sand beaches.

The sand crab, ***Emerita*** *analoga* Stimpson, is a common filter-feeding inhabitant of open coast sandy beaches on the west coasts of North & South America. This ano-

muran crab is the dominant macrofauna species of exposed beaches on the California coast (Straughan, 1983) and has been proposed as a biological indicator (Wenner. 1988). Geographic variation in size at maturity, growth rate, and reproductive biology of populations of *E. analoga* has been documented on the California coast (Efford, 1970; Fusaro, 1978; Dugan, 1990; Dugan et al., 1991; Wenner et al., 1993). The 3 to 4 month planktonic larval life of *E. analoga* (Barnes & Wenner, 1968; Dugan, unpubl.) and the lack of significant geographic trends in the expression of genetic characters reported by Beckwitt (1985) suggest that populations of *E. analoga* are not isolated on the California coast and that environmental rather than genetic factors are responsible for variation in life history and population characteristics in this species.

If the expression of life history characteristics in this well dispersed intertidal marine invertebrate is plastic, then it may be influenced by both regional and local environmental factors, including the physical characteristics of beaches. To test these predictions. we investigated relationships between geographic variation in life history traits of populations of *E. analoga* inhabiting sand beaches on the California coast and environmental factors which varied on regional and local scales. In addition, interannual variation in life history characteristics could be related to temporal variation in environmental conditions. Interannual variation in life history was investigated to evaluate the persistence of the geographic patterns observed in this species.

2. Methods

2.1. Sampling schedule and sites

Emerita analoga populations were sampled between late July and mid-August in the summers of 1983-1987 at 11 to 23 beaches (Fig. 1). *Emerita analoga* populations were sampled at sites from La Jolla, San Diego County to Morro Bay, San Luis Obispo County, California in 1983. In 1984-1987, *E. analoga* populations were sampled on beaches from San Diego County to at least as far north as Bodega Bay. Santa Rosa County. The largest geographic range surveyed was 1100 km of coast and $\approx 8^{\circ}$ of latitude from San Diego to Humboldt County in 1986. For purposes of discussion. the northern sites are the sites between Clam Beach (CB) and Pismo Beach Pier (PB), the central coast sites are those between Jalama Beach Park (JBP) and Oil Piers (OP) and the southern sites are between County Line (CL) to Scripps Beach (SBR) (Figure 1).

2.2. Population samples

Population samples were opportunistically collected from visible aggregations of crabs in the wash zone of sand beaches with a shovel and by hand. Crabs were separated from sand by sieving samples through mesh dry cleaning bags (mesh size = 1.5 mm) in seawater. Sample sizes generally exceeded 500 crabs. No estimates of density or abundance were made.

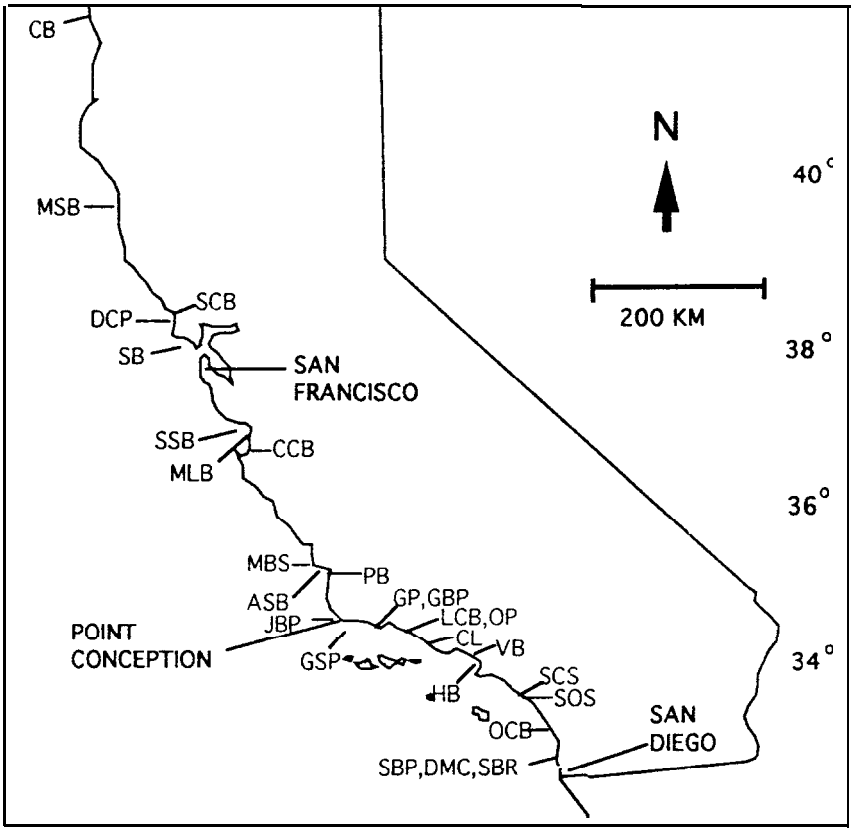


Fig. 1. Sampling locations on the California coast: Clam Beach (CB) -720 km; MacKerricher State Beach (MSB) -629 km; Salmon Creek State Beach (SCB) -487 km; Doran County Park (DCP) -481 km: Stinson Beach (SB) -308 km; Seacliff State Beach (SSB) -268 km; Moss Landing Beach (MLB) -250 km: Cannel Beach (CCB) -225 km; Morro Bay State Park (MBS) – 110 km; Avila State Beach (ASB) -84 km; Pismo Beach Pier (PB) -80 km; Jalama Beach County Park (JBP) -8 km; Gaviota State Park (GSP) + 13 km: Goleta Point (GP) + 46 km: Goleta Beach County Park (GBP) + 48 km; La Conchita Beach (LCB) + 85 km; Oil Piers (OP) + 87 km; County Line Beach (CL) + 148 km; Venice City Beach (VB) + 175 km; Hermosa City Beach (HB) + 190 km; San Clemente State Beach (SCS) + 280 km; San Onofre State Beach (SOS) + 287 km: Oceanside City Beach (OCB) + 309 km; Solana Beach Co. Park (SBP) + 330 km: Del Mar City Beach (DMC) + 332 km; Scripps Beach (SBR) + 338 km.

2.3. Population and life history characteristics

Crabs were measured with a calibrated series of sieves (Wenner et al.. 1974) to the nearest 1.0 mm carapace length (CL) to determine size-frequency distributions. All crabs above 8.0 mm CL were examined to determine sex. The reproductive condition (presence or absence of eggs) of all female crabs > 8.0 mm CL was recorded. Modal structure of each population sample was examined and general patterns in mature animals were noted. The absence of distinct gaps in many of the size-frequency distributions make it difficult to confidently distinguish the sizes of overlapping modes by graphical or computer methods, given sample sizes of < 5000, unless additional information is available about the population (Grant et al., 1987).

For each sample, four life history characteristics: the female size at maturity and the 5th and 95th percentile sizes of ovigerous female crabs and size of the largest male crab

were determined from the size-frequency distributions and used for comparisons. Female size at maturity was estimated by the smallest size class (CL) at which 50% of the female crabs were ovigerous for each population sample (Wenner et al., 1974; Dugan et al.. 1991). To compare the size ranges of ovigerous crabs, the 5th and 95th percentile sizes (CL) of ovigerous crabs were determined from the cumulative number of ovigerous crabs in each sample (see Dugan et al., 1991). Use of the 5th and 95th percentile sizes minimized the influence of extreme values. We used two measures of the size of onset of egg production in female crabs in our comparisons because in many samples the 5th percentile size of ovigerous crab was several mm smaller or larger and represented a different segment of the reproductive population than did the female size at maturity as described above.

2.4. *Physical* measurements

Coastline distance (km) of each sampling site from Point Conception was determined from two baselines drawn parallel to the coast on either side of Point Conception, an important biogeographic boundary and the location of a major change in coastal orientation from a north to south trend to a west to east trend. Point Conception is given the value of zero and values to the north of that point have negative values while those to the south have positive values as in Wenner et. al. (1993) and Dugan et al. (1991). Coastline distances were used as the independent variable rather than latitude in geographic comparisons because of the west to east orientation of the coastline of much of Southern California.

Water temperatures were measured in the surf zone at a depth of 0.5 m at each site in all surveys. Sediment samples were collected from areas where aggregated crabs occurred on each beach in the surveys of 1986 and 1987. Sediment samples were washed. dried, shaken through a series of graded sieves for 20 min. The fractions in each sieve were weighed to determine grain size distribution. Median grain size and sorting were estimated for each sample by graphical methods and expressed in Phi units (Folk. 1968). To provide a better description of the sediment characteristics at each beach for regression analyses, an index of beach sediment characteristics was calculated by dividing the grain size by the sorting coefficient. This index better characterized differences between uniformly fine sand beaches and those with poorly sorted coarse sand. Beach slope was measured in the areas where aggregations of sand crabs occurred in 1987 at all beaches and expressed as an angle in degrees.

To estimate food availability, surf zone chlorophyll ***a*** concentrations were measured at each beach during the 1987 survey.. Triplicate 500 ml water samples were taken in the surf zone (0.5m depth) and were filtered through Whatman GF/C filters containing two drops of 20% $MgCO_3$ suspension uithin 2 h of sampling. The pigments were extracted in 10 ml of 90% acetone for 20 h on the filters (Parsons et al.. 1984). Chlorophyll ***a*** concentrations were measured using the fluorometric method of Parsons et al. (1983) with a Turner Designs Fluorometer.

2.5. Data analysis

Relationships between life history characteristics of *E. analoga* and physical factors. and coastline distance were examined using Spearman's rank correlation. Interannual differences in population characteristics and water temperatures were tested using two-way analysis of variance without replication. Correlations between life history traits and surf zone water temperature were examined for the data from all years using simple linear regression analysis. For the data from 1986 and 1987, correlations between life history- traits and sediment size, sediment sorting, sediment index. beach slope (1987 only) and chlorophyll *a* (1987 only) were examined initially using simple linear regression analysis. Annual differences in. and variation between the relationships of life history traits and surf zone water temperatures were examined using analysis of covariance.

For the 1986 and 1987 surveys, when additional environmental factors were measured, multiple linear regression analysis was used to determine if the addition of other physical factors (chlorophyll *a*, beach slope, sediment size and sorting) as independent variables produced better predictions of life history characteristics than water temperature alone. The high correlations ($p < 0.0 1$) between the independent variables of beach slope, sediment grain size, sediment sorting, and the index of sediment size and sorting, precluded the incorporation of all those environmental factors into the same multiple linear regression analysis. Beach slope is considered to be a less conservative measure of beach morphodynamics than sediment characteristics (McLachlan, 1990) and the sediment index provided a more complete description of beach sediment characteristics than did sediment grain size or sediment sorting alone. Therefore, we used the index of sediment characteristics as an independent variable representing local beach morphodynamic conditions in our analyses.

3. Results

3. I. Physical characteristics and sampling effort

Sample site locations, names, and coastline distances are provided in Fig. 1. During our study, 94 population samples were collected and a total of 104 837 crabs measured.

Surf zone water temperatures varied geographically, ranging from 11.5 °C at MacKerricher State Beach to 25.6 °C at Solana Beach County Park during our study. Surf zone water temperature increased significantly with coastline distance from north to south in all years (Fig. 2, Table 1). Over the 5 y-r of our study, variation in water temperature between sites was significant and the variation between years was not significant (two-way ANOVA without replication: sites, $F = 2.10$. df = 12, $p < 0.001$, years, $F = 0.77$, df = 4, n.s.). The warmest temperatures recorded during the surveys occurred in 1983 and 1984 at beaches located south of Point Conception, particularly those sites near the southern end of the survey range where surf zone water temperatures were higher than 22.5 °C in those years. Surf zone water temperatures at sites north of Point Conception were not consistently higher in 1983 and 1984..

Other physical characteristics of the beaches, including sediment grain size, sediment

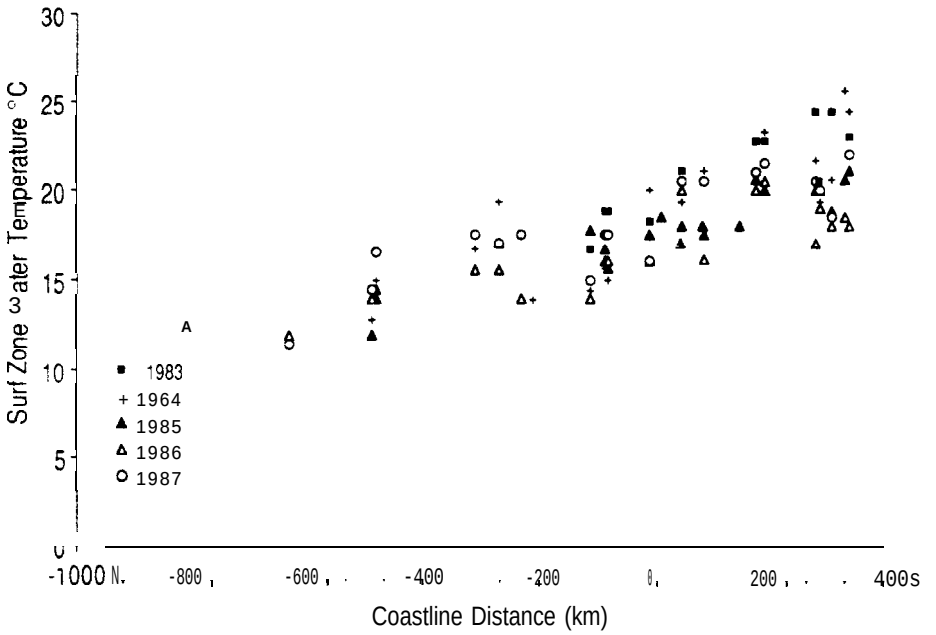


Fig. 2. Surf zone water temperature as a function of coastline distance in the midsummer surveys of 1983-1987.

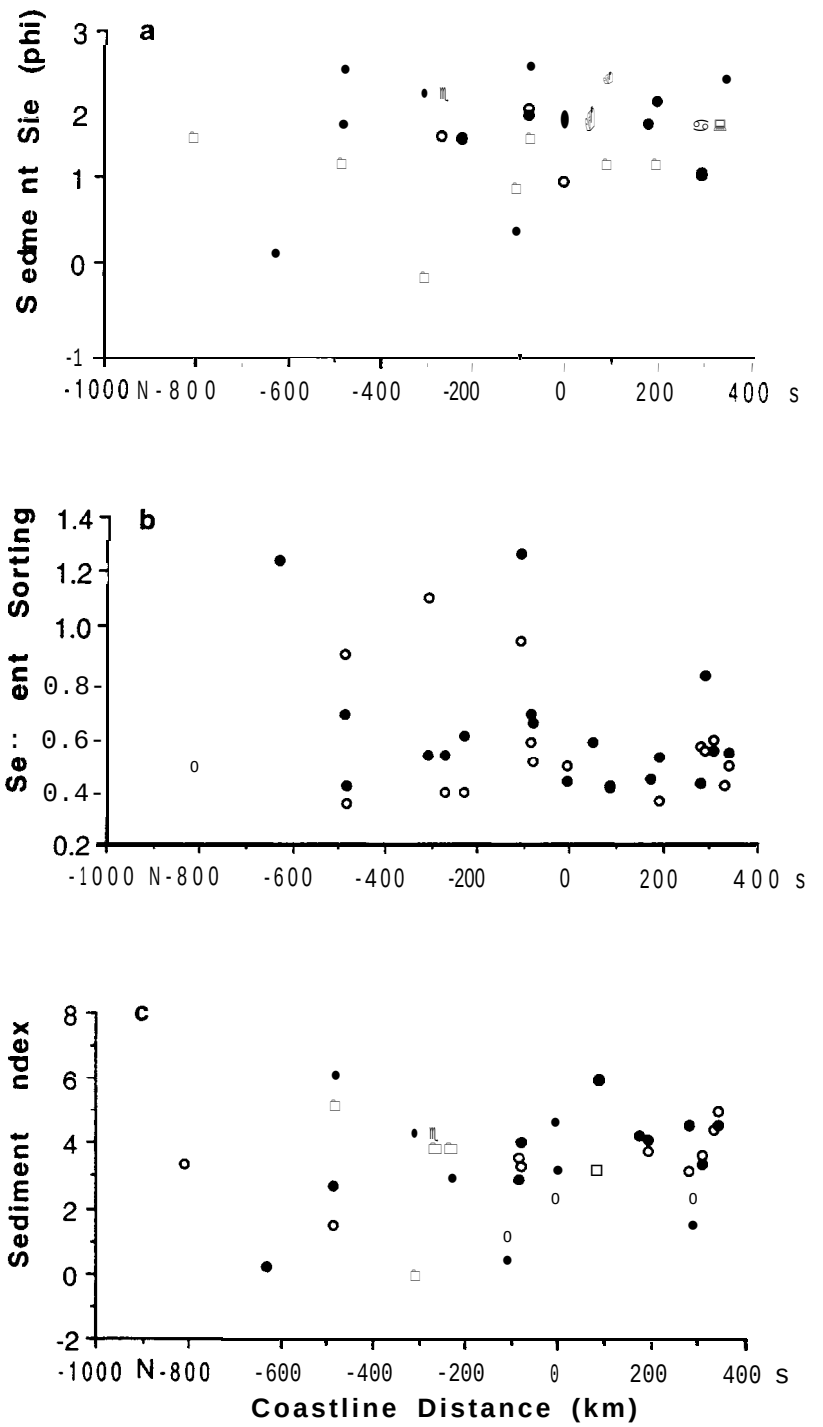
sorting, sediment index, beach slope, and chlorophyll a concentration varied considerably on local scales and exhibited no geographic patterns (Figs. 3 a-e) in the 1986 and 1987 surveys. Those physical characteristics were not correlated with coastline distance (Table 1). Median grain size ranged from fine sand, 0.18 mm (2.45 Phi), at La Jolla to coarse sand, 1.02 mm (-0. 03 Phi), at Stinson Beach in 1986. In 1987, the sediment size range was similar, 0.36 mm (2.61 Phi) at Pismo Beach to 0.83 mm

Table 1
Spcarman's rank correlation coefficients for sand crab life history traits. water temperature. beach characteristics and coastline distance for the 1983-1987 surveys

Measure	Survey year				
	1983	1984	1985	1986	1987
Female size at maturity	− 0.86**	− 0.89***	− 0.89***	− 0.89***	− 0.81***
Largest ovigerous carab	− 0.85**	− 0.85***	− 0.80***	− 0.88***	− 0.83***
Smallest ovigerous crab	− 0.80*	− 0.83***	− 0.81***	− 0.91***	− 0.80**
Largest male	− 0.64 n.s.	− 0.85***	− 0.80***	− 0.82***	− 0.88***
Temperature	0.83**	0.84***	0.93***	0.84***	0.83***
Sediment size	+	+	+	0.38 n.s.	0.112 n.s
Sediment sorting	+	+	+	− 0.00 n.s.	− 0.30 n.s.
Sediment index	+	+	t	0.23 n.s.	0.25 n.s.
Beach slope		+	+	+	0.07 n.s.
Chlorophyll *a*	+	+	+	+	− 0.39 n.s.
No. of sites	11	18	'3	20	18

* $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$ (+ = not measured).

(0.276 Phi) at MacKerricher State Beach. Sediment sorting ranged from well sorted. 0.36, at Hermosa City Beach to poorly sorted, 1.10. at Stinson Beach in 1986 and over a similar range. 0.31 at Oil Piers to 1.26 at Morro Bay State Park. in 1987. The sediment index ranged from well sorted fine sand (5.22) at Doran County Park to poorly sorted coarse sand (-0.02) at Stinson Beach in 1986 and over a similar range. 6.12 at Doran County Park to 0.22 at MacKerricher State Beach. in 1987. In 1987. chlorophyll *a* concentration ranged from 0.88 μg. 1 at San Onofre State Beach to 10.21 μg l



at Avila State Beach. Beach slopes ranged from 1.4° (flat) at several sites to 4.2° (steep) at Jalama Beach County Park in 1987.

Beach slope, sediment grain size, sediment sorting and sediment index were significantly correlated in each survey year, and between survey years in some cases. Beach slope was correlated with sediment size in 1986 and 1987 ($p < 0.01$). Sediment sorting was correlated with sediment particle size in 1986 and 1987 ($p < 0.01$). Sediment sorting was significantly correlated between years ($p < 0.05$) but sediment size was not. The sediment index (sediment grain size/sorting) was correlated with beach slope ($p < 0.01$) and was not correlated between years. In 1987, water temperature was not correlated with chlorophyll a concentration and chlorophyll a concentration was not correlated with sediment characteristics or beach slope.

3.2. Population structures

To illustrate geographic differences between populations of *E. analoga*, population structures at three sites representative of northern, central and southern beaches dur-

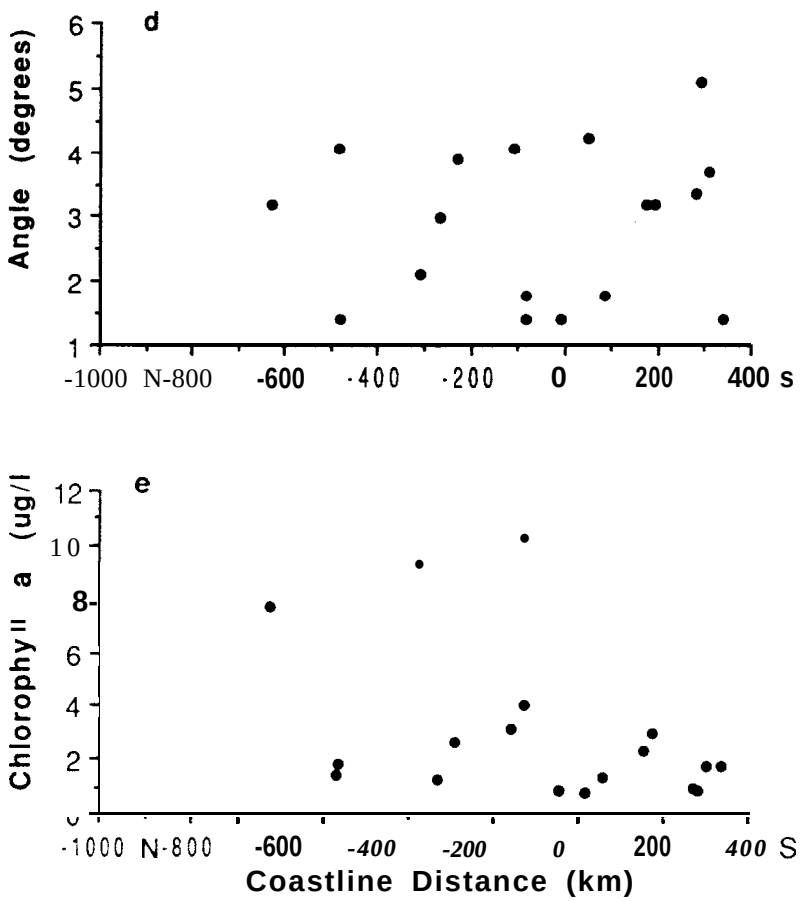


Fig. 3. Fig. 3(a). Median sediment grain size as a function of coastline distance in the midsummer survey of 1986 (○) and 1987 (●). (b) Sediment sorting as a function of coastline distance in the midsummer survey of 1986 (○) and 1987 (●). (c) Sediment index as a function of coastline distance in the midsummer survey of 1986 (○) and 1987 (●). (d) Beach slope as a function of coastline distance in the midsummer survey of 1987. (e) Surf zone chlorophyll *a* concentration as a function of coastline distance in the midsummer survey of 1987.

ing the 5 yr of our study are given in Figs. 4, 5 and 6. At individual beaches. the overall population structures of crabs > 8 mm in CL varied relatively little from year to year as illustrated by the sites shown in Figs. 4. 5 and 6, although the differences between sites persisted over time.

In general, population structures were dominated bv voung of the year crabs at all but the northernmost sites (MacKerricher & Clam Beach) in every year (e.g. Figs. 4-6). Female crabs attained larger sizes than male crabs at all sites (e.g. Figs. 4-6). The size of the smallest ovigerous crab corresponded closely to the size of the largest male crab in all samples (e.g. Figs. 4-6).

Population structures were polymodal at most locations throughout the study as seen in Figs. 4-6. Population structures varied between locations and some geographic

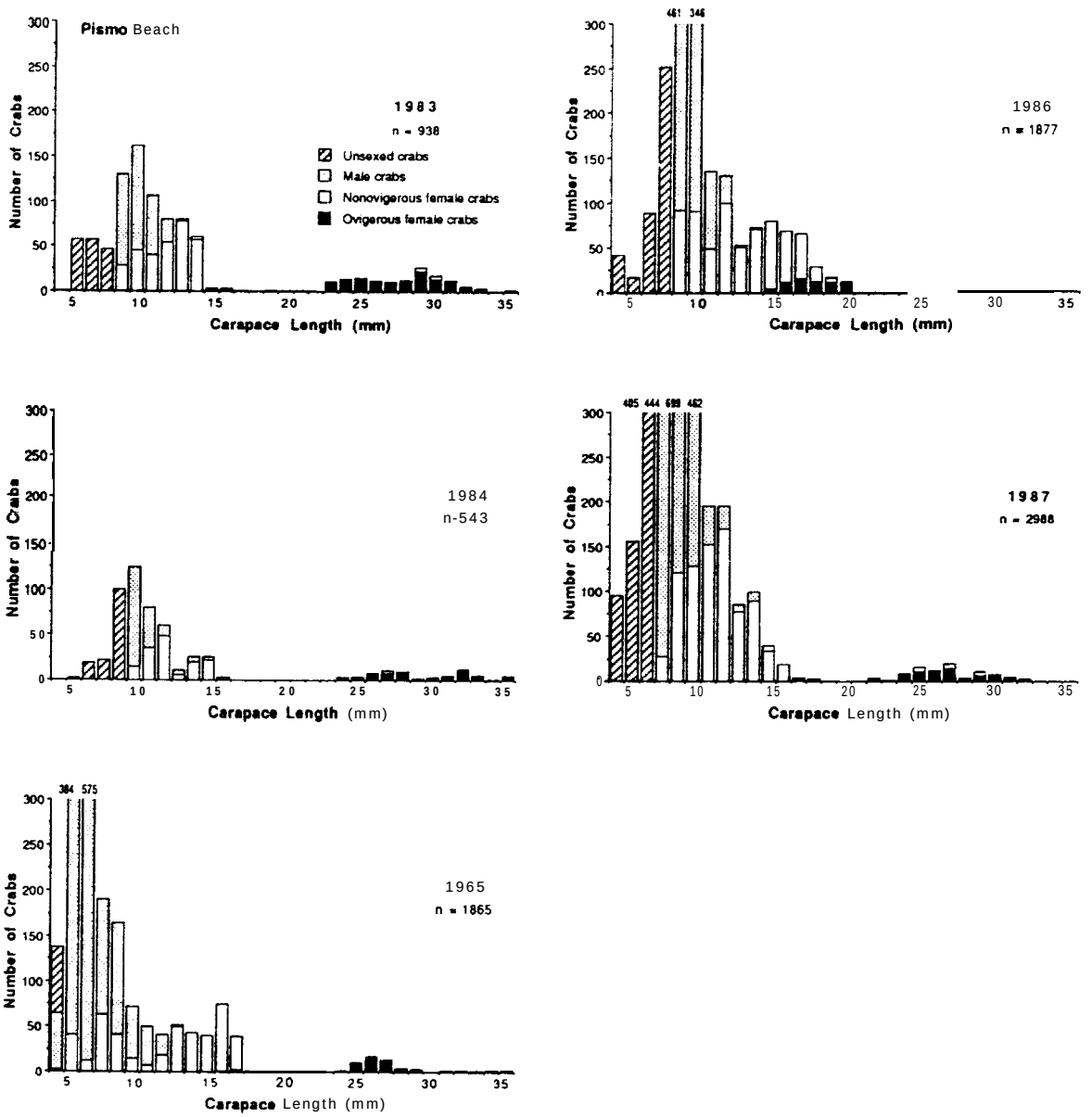


Fig. 4. Size frequency distributions of *E. analoga* at Pismo Beach Pier during the midsummer surveys of 1983-1987.

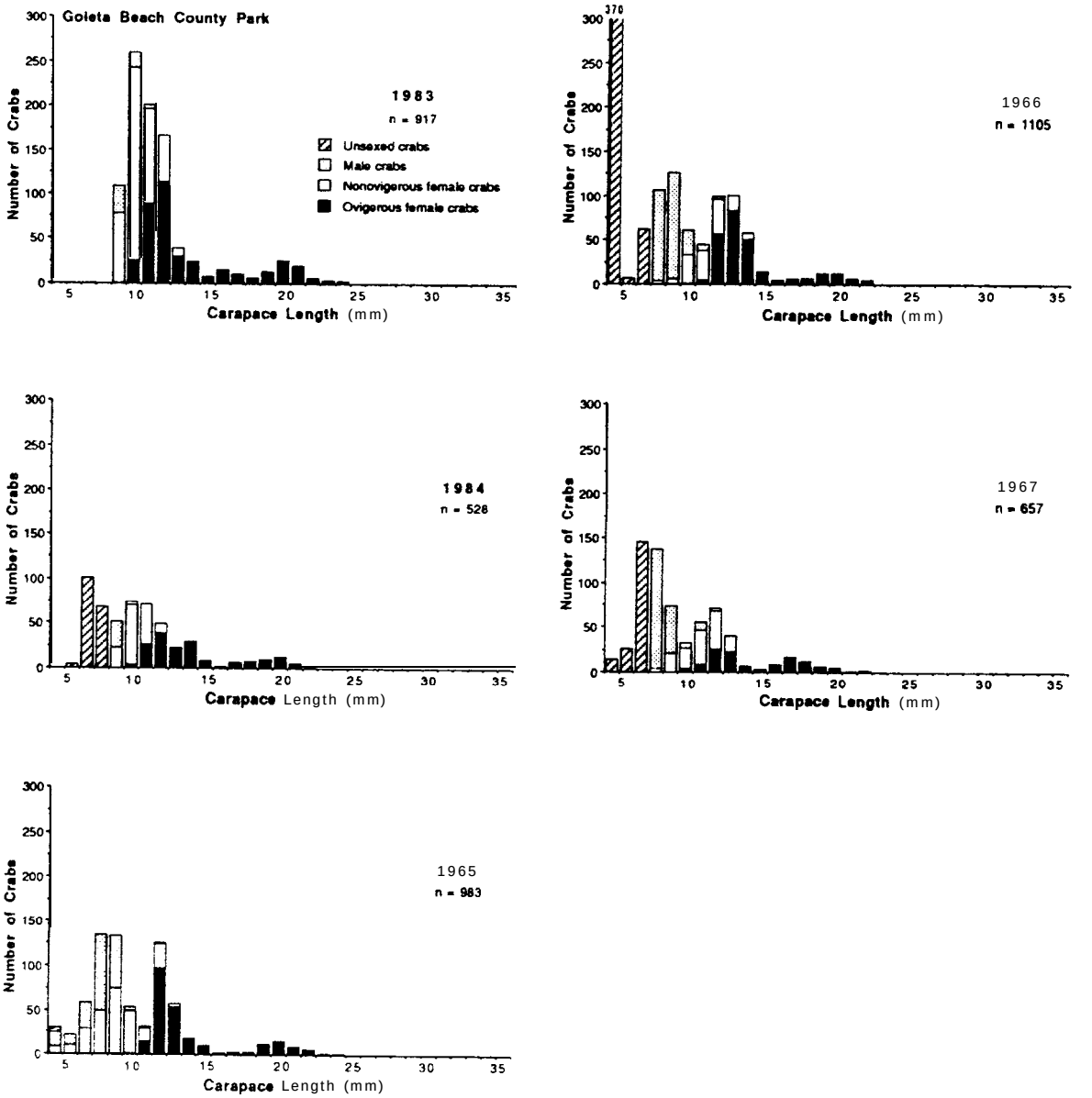


Fig. 5. Size frequency distributions of *E. analoga* at Goleta Beach County Park during the midsummer surveys of 1983–87.

patterns were evident. Size-frequency distributions of male crabs were unimodal in all samples. Two to three modes of female crabs occurred in the size-frequency distributions of populations at most of the beaches (Figs. 4-6). Female crabs in the northern and central coast populations (Figs. 4 and 5) exhibited more distinctly polymodal population structures with less overlap in size between modes evident than female crabs in populations at southernmost beaches (Fig. 6). Modes of overwintered and young of the year female crabs were separated by gaps of 2– 10 mm CL in northern populations (Fig. 4). Modes of over-wintered and young of the year female crabs were distinct, but no gaps were evident in the central coast populations (Fig. 5) and in some of the southern populations (Fig. 6). One to two modes of young of the year female crabs and a single mode of over-wintered female crabs were evident every year at all of the

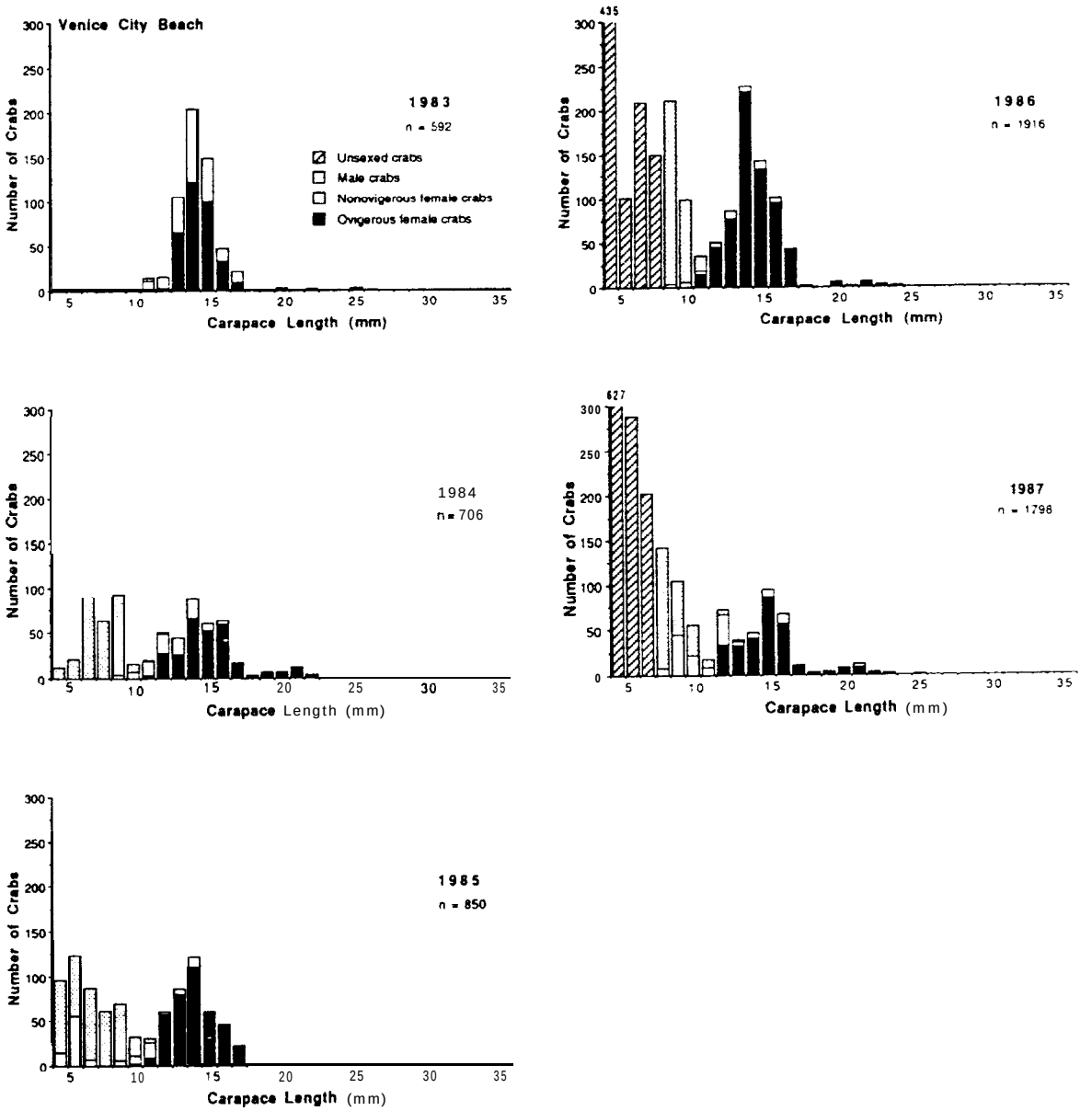


Fig. 6. Size frequency distributions of *E. analoga* at Venice City Beach during the midsummer surveys of 1983-87.

northern, central and some of the southern beaches (Figs. 4 and 5). The mode of overwintered female crabs was not well represented at the six southernmost beaches in most years of our study (San Clemente State Beach to Scripps Beach) and in some years at the other southern sites (see 1983, 1985, Fig. 6).

3.3. Geographic patterns in life history

All of the life history characteristics used in comparisons (the size at maturity of female crabs, the largest ovigerous female crab size (95th percentile). the smallest ovigerous female crab size (5th percentile), and the largest male crab size) varied

geographically. decreasing significantly with coastline distance from north to south in all of the surveys except for largest male crab size in 1983 (Figs. 7-10, Table 1). Carapace lengths of female size at maturity, smallest and largest ovigerous crabs and the largest male crab were 1.5 to 3.0 times greater in northern than in southern populations.

Female age at maturity varied geographically. Ovigerous crabs were primarily over-wintered female crabs at northern sites (Fig. 4). over-wintered and young of the year crabs at central coast sites (Fig. 5) and primarily young of the year crabs at southern sites (Fig. 6).

The life history measures were significantly correlated with each other in every survey. ($p < 0.05$). In populations where the largest ovigerous crab size was large, the female size at maturity was also large, as were the smallest ovigerous crab size and largest male crab size.

The geographic patterns in life history characteristics persisted through the 5-yr study. Data from each survey was significantly correlated with the data from all other surveys for each life history characteristic ($p < 0.01$). Variation between populations inhabiting different sites was significantly greater than the variation between years for each of the four life history measures (two-way ANOVA without replication: female size at maturity, site F = 7.91, df= 12, $p < 0.001$, year F = 0.75, df = 4, n.s., largest ovigerous crab size, site F = 13.16, df = 12, $p < 0.001$, year F = 0.73, df = 4, n.s., smallest ovigerous crab size, site F = 8.89, df = 12, $p < 0.001$, year F = 0.57, df = 4, n.s., largest male crab size, site F = 5.65, df = 12, $p < 0.001$, year F = 1.59, df = 4, n.s.)

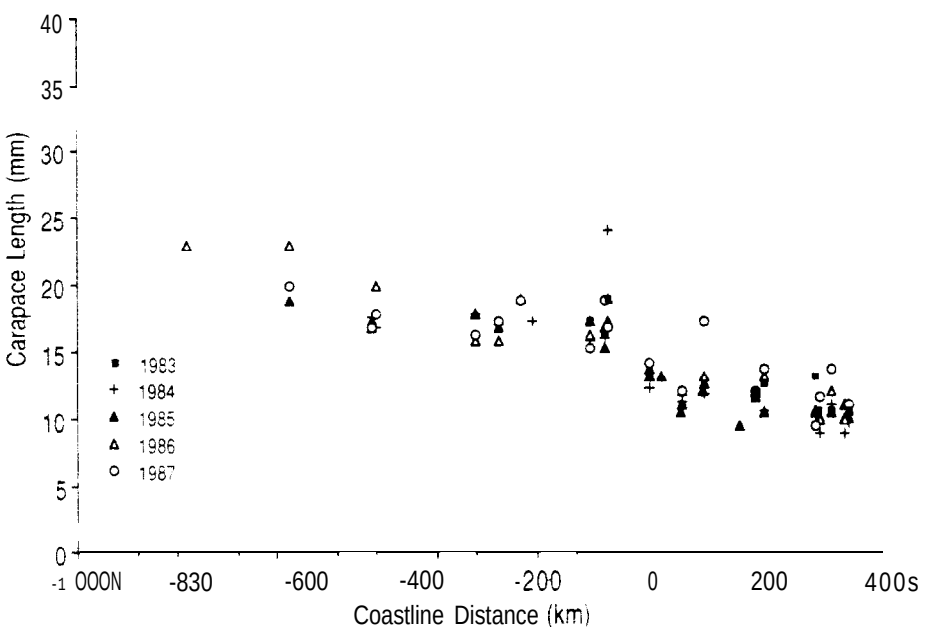


Fig. 7. Size at maturity of female crabs as a function of coastline distance for the midsummer surveys of 1983–87.

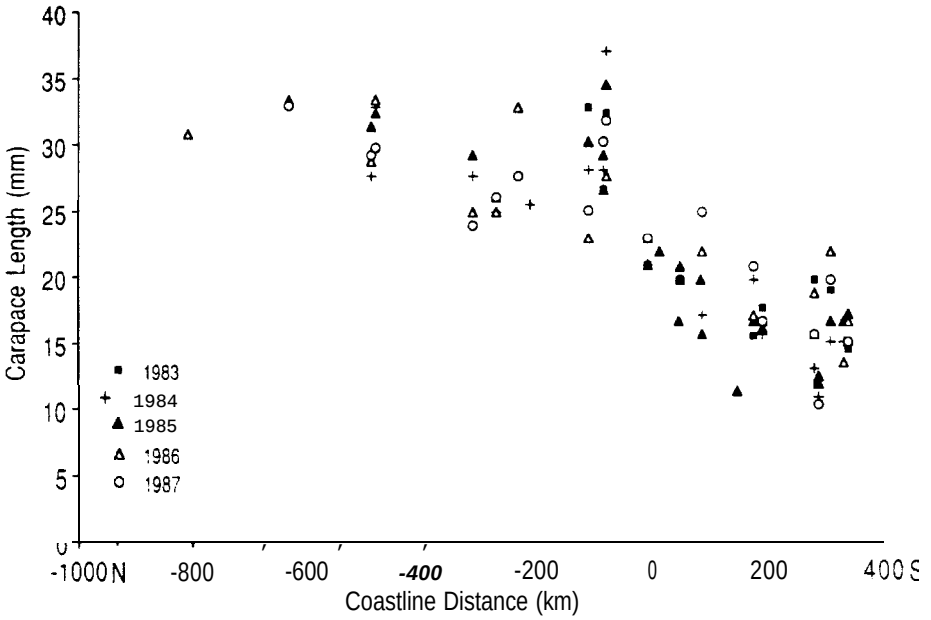


Fig. 8. Largest ovigerous crab size as a function of coastline distance for the midsummer surveys of 1983–87.

3.3. Environmental correlations

The four population life history measures were inversely correlated with water temperature in each of the five surveys (Table 2), as illustrated for size at maturity in Fig. 11. The elevations of those relationships varied significantly between years (ANCOVA, size at maturity F = 4.88, df = 4, $p < 0.01$, largest ovigerous crab size

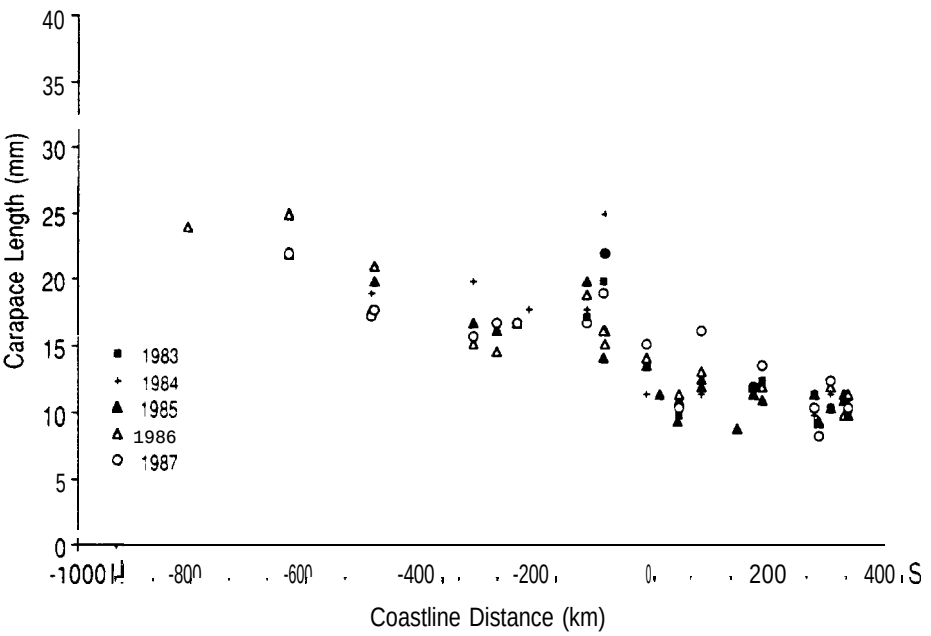


Fig. 9. Smallest ovigerous crab size as a function of coastline distance for the midsummer surveys of 1983-87.

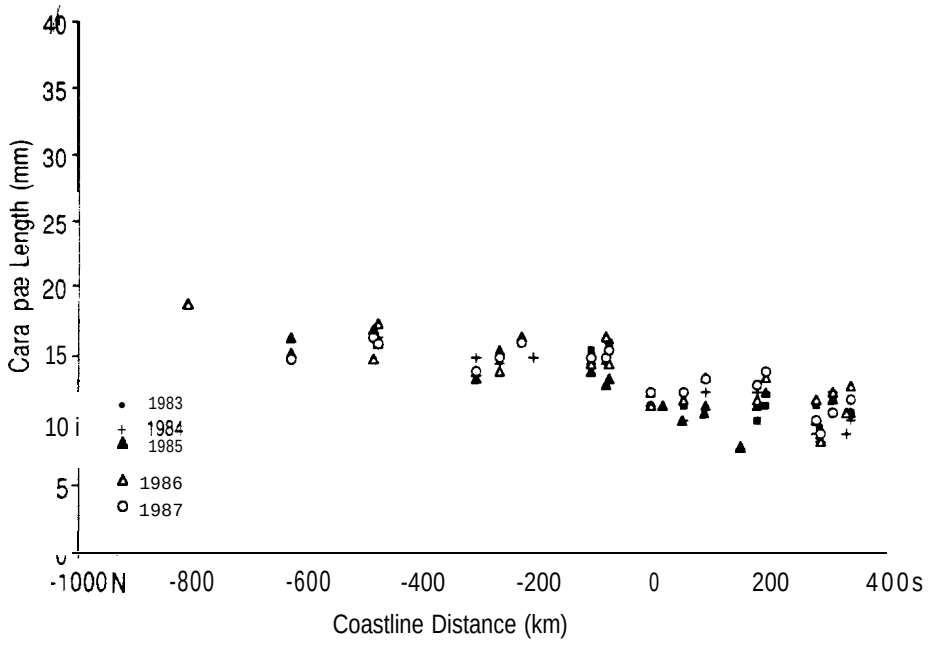


Fig. 10. Largest male crab size as a function of coastline distance for the midsummer surveys of 1983437.

F = 3.75, df = 4, $p < 0.01$, smallest ovigerous crab size F = 4.96, df = 4, $p < 0.01$, largest male crab size F = 3.81, df = 4, $p < 0.01$) but the slopes did not.

The slopes of the linear regressions between the four population life history characteristics and water temperature varied significantly between the life history measures in each of the surveys (ANOVA 1984 $F = 4.39$, df= 3, $p < 0.01$, 1985 $F = 7.21$, df = 3, $p < 0.001$, 1986 $F = 6.53$, df = 3, $p = 0.001$, 1987 $F = 3.66$, df = 3, $p < 0.05$), except for 1983. In 1983, the slopes were homogeneous but the elevations were significantly different (ANCOVA F = 14.97, df = 3, $p < 0.001$). Regressions of male crab size had the lowest slope and those of largest ovigerous crab had the greatest slope in each of the five surveys.

Female size at maturity, and the sizes of the largest ovigerous and smallest ovigerous crabs were significantly correlated with surf zone chlorophyll *a* in the 1987 survey (Table 3). No significant correlations occurred between the life history characteristics and sediment size, sediment sorting, the index of sediment characteristics or beach slope in the surveys of 1986 and 1987.

For 1986 and 1987, we incorporated the independent variables of surf zone water temperature, chlorophyll *a* concentration (1987 only) and sediment index into multiple linear regressions. The multiple regression correlation coefficients of life history characteristics were higher than those obtained in the simple linear regression models for single independent variables, in all cases in 1987 and in 3 out of 4 cases in 1986 (Tables 2–4).

Significant partial correlations of life history characteristics occurred with surf zone water temperature, the sediment index and chlorophyll a (Table 4). Significant negative partial correlations were found between surf zone water temperature and all four life history characteristics in both years (Table 4). Significant positive partial correlations occurred between some life history characteristics and the sediment index and

Table 2
Regression formulas for least squares regressions of life history characteristics and surf zone water temperatures

Year	Intercept	Slope	r	p	n
1983					
Female size at maturity	29.30	– 0.76	0.6X-l	*	11
Largest ovigerous crab	58.17	– 1.76	0.671	*	11
Smallest ovigerous crab	36.28	– 1.08	0.661	*	11
Largest malt crab	23.05	– 0.53	0.625	*	11
1984					
Female size at maturity	‘9.88	_ 0.85	0.803	***	19
Largest ovigerous crab	50.59	– 1.51	0.798	***	19
Smallest ovigerous crab	32.25	– 0.95	0.781	***	19
Largest male crab	22.50	– 0.52	0.795	***	I9
1985					
Female size at maturity	32.47	– 1.08	0.824	***	23
Largest ovigerous crab	61.48	_ 2.24	0.796	***	23
Smallest ovigerous crab	33.54	– 1.41	0.783	***	23
Largest male crab	26.10	– 0.53	0.804	***	23
1986					
Female size at maturity	39.02	– 1.46	0.895	***	20
Largest ovigerous crab	58.91	– 2.17	0.852	***	20
Smallest ovigerous crab	10.38	– 1.54	0.892	***	20
Largest male crab	27.19	-0.83	0.797	***	'0
1987					
Female size at maturity	39.02	– 0.77	0.710	***	18
Largest ovigerous crab	54.07	– 1.69	0.746	***	18
Smallest ovigerous crab	33.79	– 1.03	0.744	***	18
Largest male crab	24.04	– 0.59	0.703	***	18

* p 0.05. ** p 0.01, *** $p < 0.001$.

chlorophyll *a*. In 1986, largest male crab size was partially correlated with the sediment index. In 1987, the largest and smallest ovigerous female crab sizes were partially correlated with the sediment index. Female size at maturity and the smallest ovigerous crab size were partially correlated with surf zone chlorophyll *a* concentration in 1987.

4. Discussion

Strong geographic trends in several life history characteristics persistently occurred in populations of ***E. analoga*** on the Pacific coast of North America. The distinct geographic patterns demonstrated for *E. analoga*, a marine species with a long planktonic larval life, supports the hypothesis that life histories of sand crabs are plastic and

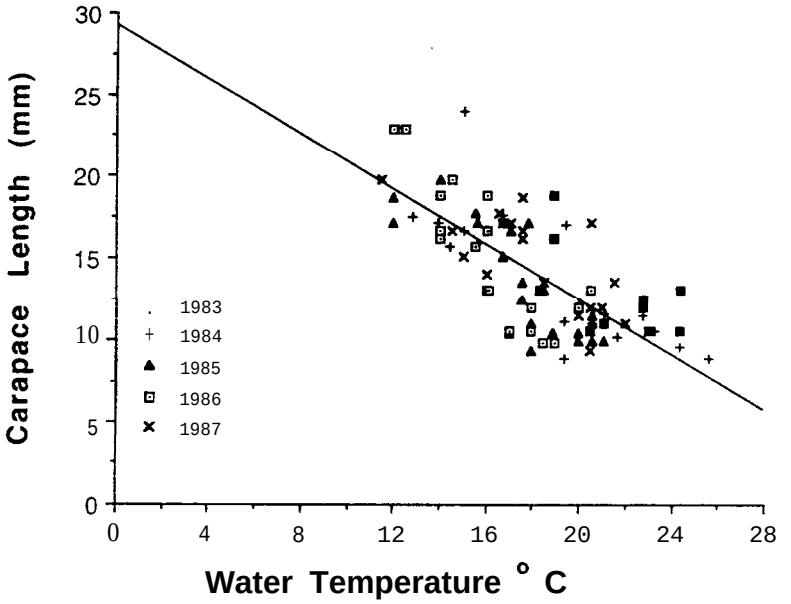


Fig. 11. Size at maturity of female crabs as a function of surf zone water temperature for the midsummer survey of 1983–87. overall linear regression: $y = -0.84x + 29.3$. $r = 0.73$. $n = 90$. Regression equations for individual years appear in Table 2.

respond to environmental variation; leading to a variety of possible life history patterns on both local and regional scales.

The significant north to south trends found in life history characteristics of *E. analoga* populations were not unexpected in view of general predictions of latitudinal and temperature-related patterns in marine invertebrates (e.g. Bergmann's Rule: Mayr, 1942; Ray, 1960) and earlier studies of *E. analoga* populations in California, including older (Cox & Dudley. 1969: Eickstaedt, 1969) and more recent studies (Wenner et al.. 1985: Wenner. 1988: Dugan. 1990; Dugan et al.. 1991: Wenner et al.. 1993). The patterns we found also agree well with the latitudinal trends of increasing size at maturity with increasing latitude reported for *E. analoga* in South America (Osorio. 1967: Eickstaedt. 1969).

Geographic variation in life history characteristics of *E. analoga* populations was correlated with regional variation in surf zone water temperature. Water temperature

Table 3
Regression formulas for least squares linear regressions of life history characteristics and chlorophyll *a* in 1987

Characteristic	Intercept	Slope	*r*	*n*
Chlorophyll a				
Female size at maturity	13.39	0.55	0.54*	18
Largest ovigerous crab	'0.33	1.02	0.47*	lb
Smallest ovigerous crab	12.98	0.71	0.54*	18
Largest male crab	12.36	0.3-l	0.42 n.s.	18

* $p < 0.05$

Table 4
Results of multiple linear regression of sand crab lift: history characteristics and environmental variables in surveys of 1986 and 1987

Life history characteristic	Multiple r	Constant		Temperature		Sediment index		Chl. *a*	
		coef.	*t*-statistic	coef.	*t*-statistic	coef.	*t*-statistic	coef.	*t*-statistic
Female size at maturity									
1986	0.89***	39.36	11.16***	– 1.60	7.23***	0.49	i 37 n.s.		
1987	0.82***	26.32	7.42***	– 0.86	3.97***	0.60	1.76 n.s.	0.37	2.14*
Largest ovigerous crab									
1986	0.87***	61.99	9.74***	– 2.58	6.46***	1.01	1.56 11.5.	+	
1987	0.86***	50.92	7.71***	– 1.96	5.18***	1.68	2.65**	0.6 1	1.87
Smallest ovigerous crab									
1986	0.90***	'4.33	11.84***	– 1.57	7.54***	0.32	0.94 n.s.	+	
1987	0.85***	30.71	7.53***	– 1.11	4.77***	0.87	2.24*	0.46	2.29*
Largest male crab									
1986	0.83***	27.52	9.42***	– 0.99	5.38***	0.65	2.20*		
1987	0.76***	22.98	7.46***	– 0.63	7.59***	0.37	1.27 n.s.	0.17	1.13 n.s.

* $p < 0.005$. ** $p < 0.0$ 1. *** $p < 0.001$ (two-t&d). n.s., not significant; + not measured.

alone may not affect life history characteristics per se but may reflect regional patterns of oceanographic conditions and productivity (Parrish et al.. 1981) on the California coast. Inverse relationships between size at maturity and water temperature, such as those found in our study. have been reported for some decapods (e.g. Templeman. 1936; Davis, 1975; Annala et al., 1980; Campbell & Eagles, 1983). However, positive relationships with water temperature (e.g. Somerton. 1981; Jewatt et al., 1985; Hines, 1989) or a lack of relationships (e.g. Campbell & Robinson, 1983; Beyers & Goosen, 1987; Hines, 1989) have also been reported in decapods.

Positive relationships were found between life history characteristics and environmental factors that did not vary regionally in our data. Positive correlations between life history characteristics and food availability, surf zone chlorophyll a, imply that as food availability increases. female size at maturity, and smallest and largest sizes of ovigerous sand crabs increase. The positive correlations of life history characteristics with an indicator of beach morphodyanamics, the sediment index, once variation resulting from temperature and food availability were removed. imply that as sediments become finer and better sorted and beach slope becomes shallower the smallest and largest sizes of ovigerous crabs and the size of the largest male crab increase.

Incorporating regionally and locally varying environmental factors into our regression model provided a better predictor of sand crab life history characteristics than any single factor. It is concluded that geographic variation in the life history characteristics of *E. analoga* populations is related to a combination of regional differences in water temperature and associated oceanography and local differences in beach morphody-

namics, as reflected by the index of sediment grain size and sorting, and productivity as reflected by surf zone chlorophyll *a* concentrations.

Life history characteristics of sand beach macrofauna populations have been correlated with water temperature and food availability in earlier studies (Wade, 1968; Wenner et al., 1987: Dugan. 1990; Dugan et al.. 1991; Wenner et al., 1993) but have never been correlated with the morphodynamics of beaches. The partial positive correlations between life history characteristics of *E. analoga* measured in this study and sediment size and sorting provide new evidence for the influence of sand beach morphodynamics on the life history of macrofauna. This conclusion is supported by the finding of a significant correlation between size at maturity and a combination of sediment grain size and surf zone water temperatures in *E. analoga* populations inhabiting eight beaches on one of the California Channel Islands (Dugan et al.. 1994).

Exposed sand beaches have been classified into a range of morphodynamic types from dissipative to reflective on the basis of physical factors, including average wave regime. beach slope, and sediment grain size (Short & Wright, 1983; McLachlan, 1990; McLachlan et al., 1993). On reflective beaches, waves break directly on shore and surge up the beach resulting in a relatively inhospitable habitat for macrofauna. Reflective beaches have coarse, poorly sorted sediments and steep slopes. Dissipative beaches are flatter with fine, well sorted sand and broad surf zones that dissipate incoming wave energy and provide a more benign habitat for macrofauna. The beaches we surveyed were intermediate in morphodynamic type and had fine to medium grain sizes, moderate to heavy wave action, and intermediate to flat slopes (*sensu* Short & Wright. 1983; McLachlan, 1990).

Beach morphodynamics have been correlated with the structure of sand beach macrofauna communities (e.g. McLachlan. 1990) but not with the life history of individual macrofauna species. The species diversity, total abundance and total biomass of macrofauna communities generally increases from reflective to dissipative type beaches (McLachlan. 1990: Jaramillo & McLachlan. 1993: McLachlan et al.. 1993). Our results suggest that beach morphodynamics. particularly those reflected by sediment characteristics, affect the population biology and life history of individual species as well. However. the trend of larger size in E. *analoga* inhabiting more dissipative beaches with finer and better sorted sand is the opposite of that found for sand beach communities and sand beach crustaceans (McLachlan. 1990; McLachlan et al.. 1993). In those comparisons, the mean individual body size of macrofauna in general. and of crustaceans as a group. increased from flat. fine sand. dissipative beaches to steep. coarse sand, reflective beaches. Similarly. Jaramillo & McLachlan (1993) found mean individual size of the isopod *E. hirsuticauda* increased significantly from flat to steep profile beaches and there were no correlations between the sizes of *E. analoga* or the isopod. *Excirolana brasiliensis*, with beach characteristics. The contrast of those trends to our results implies that for some macrofauna species inhabiting sand! beaches. population level responses to variation in beach morphodynamics may differ markedly from community level responses.

The filter-feeding behavior and swash zone habitat of *E. analoga* may contribute to this trend. A dissipative type beach may provide more favorable conditions for filter-feeding macrofauna than more reflective type beaches (Donn et al.. 1986). Beaches with

relatively flat slopes and finer sediments have longer swash periods and lower wave action on the beach face itself. The wider surf zones of flat beaches may also retain nutrients and have enhanced nearshore productivity relative to beaches with narrow surf zones (Donn et al.. 1986). The water flow patterns and benign swash climate on flat beaches provide longer feeding times for filter-feeders. In addition. lower energy expenditures are required to maintain position in the swash zone on the beach face. Fine. well sorted sand may provide a more stable substratum for burrowing and survival in high surf conditions than coarse poorly sorted sand. These factors could contribute to enhanced growth and survival of macrofauna. such as ***E.*** *analoga*. on flat fine sand beaches. For example. the largest crabs occurred on the flattest beach with the finest sand in the northern area of our study. Pismo Beach. It is hypothesized that other intertidal filter feeding beach macrofauna species. particularly those that inhabit the swash zone. such as the bivalves. *Tivela* and *Donax*. would respond similarly to variation in beach morphodynamics and swash climate. It is suggested that such patterns in the life history of dominant macrofauna species could contribute to the observed trends of increasing community biomass and abundance from reflective to dissipative beach types (e.g. McLachlan. 1990).

The phenotypic expression of a single life history characteristic in a population or individual may be related to a variety of intrinsic factors including the timing of settlement. size at settlement. growth rate. survival and allocation of resources to growth and reproduction. The covariance of the life history characteristics of *E. analoga* measured in our study suggests that similar mechanisms operate upon the growth rates, size, maturation and survival of sand crabs to produce the geographic patterns observed in our study. The observed patterns in life history characteristics were correlated with environmental factors which could have strong effects on growth rates of a filter feeder such as ***E.*** *analoga*. For example. temporal and geographic variation in molt increments of ***E.*** *analoga* are positively correlated with food availability estimated by surf zone chlorophyll a concentration (Dugan, 1990). It is suggested that growth rate from the time of settlement to sexual maturity, the age at sexual maturity and subsequent survival to the second year on the beach are correlated and contribute to the geographic patterns observed in life history traits of populations of ***E.*** *analoga*. Crabs inhabiting more productive, dissipative type beaches in cooler regions grow faster, mature later at a larger size. and may experience higher overwintering survival than crabs inhabiting less productive and more reflective beaches in warmer regions.

Geographic variation in life history patterns as shown here. could result in large regional differences in reproductive output and generation times between northern. central. and southern populations of ***E.*** *analoga* (Dugan et al.. 199 1). Our results suggest that the influence of spatial variation in beach characteristics on life history could contribute to local differences in reproductive output of populations of E. *analoga*. On steep, coarse sand beaches where growth and survival are lower, maturation occurs at smaller sizes resulting in lower lifetime reproductive output. On flat. fine sand beaches, reproductive maturity occurs at larger sizes and lifetime reproductive output may be higher. The persistence of the described patterns over time implies that the larval production in California may be dominated by E. *analoga* populations inhabiting cool productive waters and/or flat beaches with fine sand.

Aspects of the life history of ***E. analoga*** respond quite differently to environmental factors, rendering them exceptionally sensitive indicators of environmental conditions on a variety of spatial (Siegel & Wenner, 1984; Wenner, 1988; Dugan et al., 1991) and temporal scales ranging from seasonal variation (Dugan, 1990) to global warming. For example, the strong 1982-3 ENS0 (El Nino Southern Oscillation) in the eastern Pacific (McGowan. 1984) resulted in higher surf zone water temperatures in Southern California, but did not significantly alter the geographic patterns observed in life history characteristics of *E. analoga* in the present study. However. other population attributes of ***E. analoga*** in southern California, including the length of the reproductive season (Dugan. 1990). the proportions of abnormal egg masses (Siegel and Wenner. 1984: Wenner. 1988). and recruitment strength (Siegel. unpubl.). were apparently significantly affected by the changes in oceanographic conditions associated with the 1982– 1983 ENS0 (El Nino Southern Oscillation).

The apparent plasticity. of life history characteristics in ***E. analoga*** demonstrated in the present study and others (Dugan, 1990: Dugan et al., 1991). the dynamic nature of exposed sandy beach habitats (McLachlan, 1990) and the coastal oceanography of California (McGowan 1984) did not lead us to expect the patterns we observed in life history to be consistent over time. That consistency implies that the interactions between environmental factors, such as temperature, productivity and beach morphodynamics. and mechanisms, including the time of recruitment to beaches, growth to maturity and survival formed a relatively predictable pattern at individual beaches on the California coast, producing similar population structures at each beach during the 5 yr of our study.

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