

Local variation in populations of the sand crab *Emerita analoga* on sandy beaches in southern California

Variación local en poblaciones de *Emerita analoga* en playas arenosas del sur de California

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ABSTRACT

To investigate the effect of beach morphodynamics on the biology of a dominant macroinfaunal species we compared the abundance, biomass, size structure and life history characteristics of populations of the sand crab *Emerita analoga* (Stimpson) from 12 beaches representing low intermediate to dissipative types over a restricted geographic area (52 km of coastline). We found significant spatial variation in abundance, biomass, size structure and life history between populations. These parameters were not correlated with any single environmental factor including: beach morphodynamic type, water temperature, beach slope, sediment size, and sediment sorting and diversity. A significant amount of the variation in abundance, size and life history characteristics was associated with location, expressed by coastline distance. Once variation associated with coastline distance, was removed, some life history characteristics were partially correlated with water temperature, beach slope and sediment diversity. Our results suggest that variation observed in the population biology of *Emerita analoga* may be related in part to spatial variation in recruitment, growth rates and survival.

Key words: abundance, biomass, life history, beach morphodynamics.

RESUMEN

Para investigar el efecto de la morfodinámica de playas sobre la biología de una especie dominante de la macroinfauna, se comparó la abundancia, biomasa, estructura de tallas y características de historia de vida de *Emerita analoga* (Stimpson) en 12 playas arenosas (intermedias bajas a disipativas) en un área geográfica restringida (52 km de costa). Se encontró variación espacial significativa en abundancia, biomasa estructura de tallas e historia de vida entre poblaciones. Estos parámetros no estuvieron correlacionados con ningún factor ambiental, incluyendo: tipo morfodinámico de playa, temperatura del agua, declive de la playa, tamaño, sorteo y diversidad del sedimento. Una cantidad significativa de la variación en abundancia, tamaño corporal y características de historia de vida estuvo asociada a localización de sitios (distancia a lo largo de la costa). Una vez que la variación asociada con la distancia a lo largo de la costa fue removida, algunas características de historia de vida estuvieron parcialmente correlacionadas con temperatura del agua, declive de la playa y diversidad del sedimento. Nuestros resultados sugieren que la variación observada en la biología poblacional de *Emerita analoga* puede ser relacionada en parte a la variación espacial en reclutamiento, tasas de crecimiento y sobrevivencia.

Palabras clave: abundancia, biomasa, historia de vida, morfodinámica de playas.

INTRODUCTION

Intertidal sand beach macrofauna communities are believed to be structured primarily by physical processes (e.g. McLachlan 1990, McLachlan et al. 1993). For these communities, patterns of increasing species richness, abundance and biomass from reflective to dissipative sand beaches (expressed as Dean's parameter, or Beach State Index)

have been described for beaches around the world (McLachlan 1990, McLachlan et al. 1993, Jaramillo & McLachlan 1993, McLachlan et al. 1996). Mean individual size has been shown to decrease across the gradient from reflective to dissipative beaches (McLachlan 1990).

Physical processes associated with beach morphodynamics may affect the population biology of individual species of macrofauna

in a similar manner (Jaramillo & McLachlan 1993). Variation in abundance, biomass and mean individual size of populations of dominant species can contribute to variation in community structure and the described community patterns. The abundance and distribution of individual sand beach macrofauna species have been related to physical factors which vary on local scales, including grain size, swash circulation, and food availability (e.g. Sastre 1984, Bowman & Dolan 1985, Shepherd et al. 1988). Only one study has investigated population responses to beach morphodynamic type (Jaramillo & McLachlan 1993).

Emerita analoga (Stimpson) is a filter-feeding intertidal decapod which occurs in high abundances on a variety of beach morphodynamic types on the west coasts of North and South America (Dugan et al. 1995, Jaramillo & McLachlan 1993). It is the most abundant and widespread macrofauna species on Southern California beaches (Straughan 1983). Earlier studies of *Emerita analoga* in North (Efford 1969, 1970, Fusaro 1978, Siegal & Wenner 1984, Dugan 1990, Dugan et al. 1991, 1994, Wenner et al. 1993) and South America (Osorio 1967, Jaramillo & McLachlan 1993) indicate that this species is an excellent choice for investigating the response of individual species to beach morphodynamics and evaluating their role in community patterns.

The results of earlier studies suggest that life history characteristics of *Emerita analoga* may respond to beach morphodynamics (Dugan 1990, Dugan et al. 1991, 1994). Variation in life history of *Emerita analoga* populations over a wide geographic range on the California coast (1200 km) was inversely correlated with regional gradients in surf zone water temperature and partially correlated with factors which did not vary regionally, including food availability, sediment grain size, sorting and beach slope (Dugan 1990, Dugan et al. 1994). Crabs were largest in size on flat beaches with fine sand and decreased in size as slope and sediment grain size increased suggesting that the life history of sand crab populations may respond in part to beach morphodynamic type. Over a narrower geographic range, comparisons of populations inhabiting 8 beaches on an off-

shore island found variation in life history was correlated with a combination of water temperature and sediment characteristics, also indicating that beach morphodynamic type may contribute to variation in life history (Dugan et al. in press). The correlations of crab size and sediment size found in those studies, suggested that the individual size of *Emerita analoga* increased toward increasingly dissipative conditions, a pattern opposite to that described for macrofauna communities (McLachlan 1990).

The present study was designed to test the hypothesis that aspects of the population biology and life history of a dominant macrofauna species are influenced by beach morphodynamics and to evaluate the relative effect of beach morphodynamics on an individual species. We investigate this hypothesis by examining relationships between the abundance, biomass, population biology and life history of *Emerita analoga* and physical factors including beach morphodynamic state over a narrow geographic range.

METHODS

Population samples of *Emerita analoga* were collected on 12 beaches in Santa Barbara and Ventura Counties between August 18 and 30, 1994 (Fig. 1). Samples of crabs were collected on falling tides, one to two hours before the afternoon low tide. One to three sites were sampled in the afternoon of each of the following days: August 18, 19, 20, 22, 24, 26, 29, 30. The zone of occurrence of *Emerita analoga* was determined at each site by preliminary sampling along a transect from the mid-beach through the swash zone to a depth of approximately -0.5 m.

Three replicate samples of crabs were collected at each beach. The locations of the replicates along the beach were selected randomly but a gap of at least 5 meters was placed between the sample lines to reduce disturbance of crab aggregations. For each sample, a series of cores (0.1 m diameter by 0.1 m depth every 0.25 meter) were taken in a straight line perpendicular to shore from the highest to the lowest level of crab occurrence. Equal numbers of cores were taken for each sample line at a site. Cores were

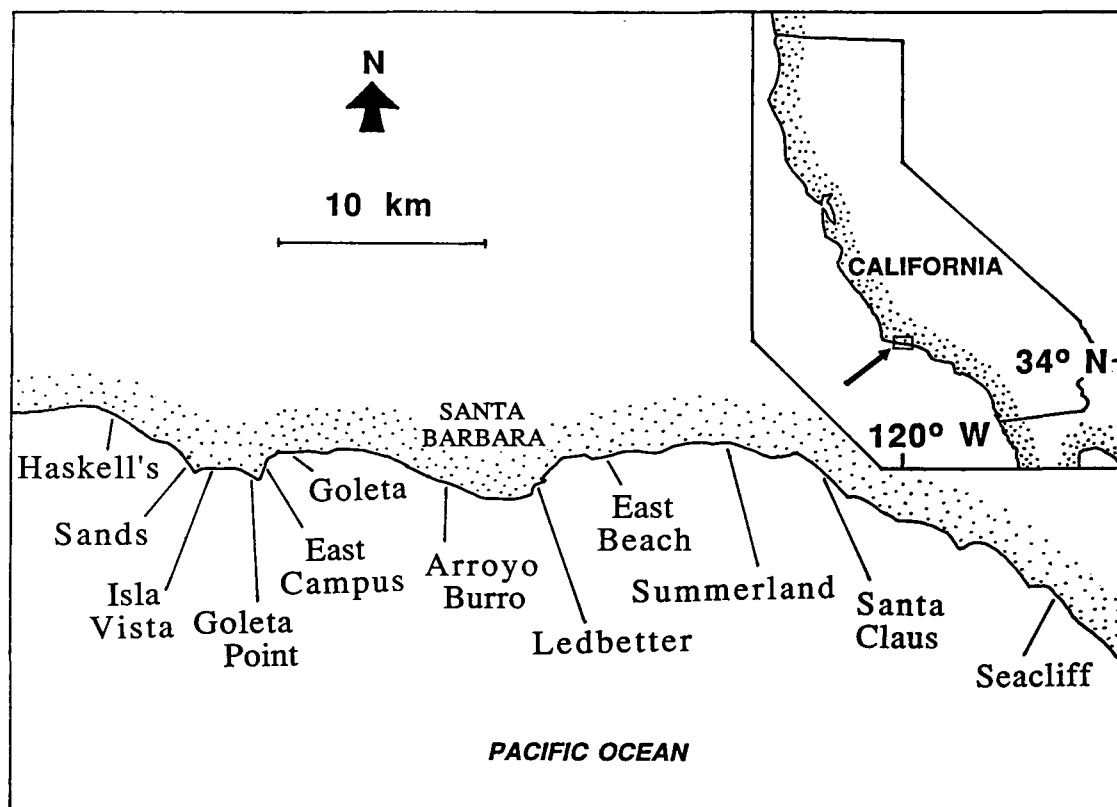


Fig. 1: Map of the California coast near Santa Barbara showing the region of the study (inset) and the locations of the beaches sampled. For beaches from west to east, the pooled sample sizes are: 1035, 315, 674, 1274, 657, 318, 649, 113, 603, 315, 191, 191.

Mapa de la costa de California cerca de Santa Bárbara mostrando la región del estudio (inserta) y localización de playas muestreadas. Para playas de oeste a este los tamaños de las muestras combinadas son: 1035, 315, 674, 1274, 657, 318, 649, 113, 603, 315, 191, 191.

taken in rapid sequence through the crab aggregations to reduce escape by disturbed animals. Cores were pooled across the zone of occurrence, placed in a mesh dry cleaning bag (1.5 mm mesh size) and rinsed in seawater to separate crabs and megalopa from the sand. For samples with more than 1 kg of coarse sediments retained, samples were elutriated to separate animals from the sediments. Samples of live crabs were transported to the laboratory for measurement.

Samples of live crabs were counted, blotted dry and weighed to the nearest 0.1 g to determine abundance and wet biomass. Samples of 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. The numbers and biomass of ovigerous crabs and megalopa were measured. Num-

bers of megalopa (post-larvae) were used to estimate abundance of new recruits (≤ 1 month on the beach). Numbers of overwintered crabs and young of the year crabs were determined by examination of size frequency distributions as in Dugan et al. (1991). Dry biomass estimates were calculated as 25% of the wet biomass (McLachlan, personal communication). Means of abundance and biomass data for each sample were calculated per running meter of beach as suggested by Brown & McLachlan (1990).

Four life history characteristics were determined from the size frequency distributions for each sample: female size at maturity, sizes of the smallest and largest ovigerous crabs (the 10th and 90th percentile sizes respectively) and the size of the largest male crab and reported as carapace length (CL)

as in Dugan et al. (1991, 1994). Means of life history characteristics were calculated for the 3 samples for each beach.

Coastline distances between sampling locations were determined on a map. We measured a number of physical factors for each of the three sample lines at a beach. Seawater temperature was measured in the surf zone (~ 0.5 m depth) and at the water table outcrop. Salinity was measured in the surf zone and at the water table outcrop.

Sediment samples were collected at the water table outcrop for each sample line. Sediment samples were rinsed with distilled water, dried, and shaken through standard sieves. The fractions in each sieve were weighed to determine grain size distribution. Mean grain size and IGSD (inclusive graphic standard deviation) were determined (Folk 1968). Sediment diversity was calculated using the Shannon Weiner diversity index (Zar 1984) as in Etter & Grassle (1992). Beach slopes were measured at the strand line and at the water table outcrop for each sample line and expressed as 1/gradient. Breaker height (m) and wave period (sec) of 5 set waves were measured for each sample line at each location. Dean's parameter, a dimensionless index of fall velocity, was calculated from the mean breaker height divided by mean wave period and sand fall velocity (Short & Wright 1983). Sand fall velocities were calculated using the conversion given by Gibbs

et al. (1971) and the mean sand particle size for each sample.

One way analysis of variance was used to determine if variation in population characteristic between locations was greater than that within locations. For population characteristics with very low or no variance, a non-parametric one way analysis of variance (Kruskall-Wallis) was used. Relationships between population data and physical factors, and coastline distance were examined using Spearman's rank correlation. Correlations between population characteristics and physical factors were investigated using simple linear correlation analysis. Multiple linear regression analysis was used determine if a combination of uncorrelated physical factors (coastline distance, water temperature, sediment diversity and beach slope) produced better predictors of population characteristics than single factors.

RESULTS

Names, locations, pooled sample sizes and coastline distances of sampling locations are provided in Fig. 1 and Table 1. During the study, we collected 36 population samples from 12 beaches and measured 6335 crabs.

The environmental factors measured at the time of sampling varied between locations (Table 1) but did not vary significantly with

TABLE 1
Coastline distances and physical characteristics of beaches sampled for *Emerita analoga* in August 1994. Each value is the mean of 3 sample lines
Distancia de la costa y características físicas de las playas probadas para *E. analoga* en agosto de 1994. Cada valor es el intermedio de tres líneas probadas

Location	Distance km	Water Temp. °C	Mean Grain Size µm	Sediment Diversity H'	Beach Slope 1/gradient	Wave Height m	Wave Period s	Dean's Parameter
Haskells	0.0	21.0	252	0.393	10	0.8	8	2.9
Sands	4.2	21.6	219	0.308	31	1.5	7	6.9
Isla Vista	5.3	21.9	180	0.347	15	0.4	10	1.4
Goleta Point	7.3	23.2	261	0.424	11	1.1	7	4.2
East Campus	8.3	22.4	222	0.375	12	0.3	7	1.5
Goleta	9.9	22.8	314	0.588	9	0.4	7	1.2
Arroyo Burro	17.9	22.2	197	0.362	18	0.6	7	3.2
Ledbetter	22.4	22.6	208	0.368	15	0.4	7	1.8
East Beach	26.7	20.9	256	0.339	8	0.9	7	3.4
Summerland	32.7	21.2	221	0.313	10	0.9	7	4.1
Santa Claus	37.9	22.8	223	0.367	22	1.2	9	4.2
Seacliff	51.5	21.3	184	0.242	27	0.6	8	3.0

coastline distance (Spearman's rank correlation $P > 0.05$). Surf zone water temperatures varied from 20.9 to 23.2° C. Mean sediment grain size ranged from 180 to 314 μ m and sediment diversity from 0.242 to 0.588. The beach slope (1/gradient) varied from 8 to 31. Dean's parameter values varied from 1.2 (low intermediate) to 6.9 (dissipative), all but one of the beaches sampled were intermediate in morphodynamic state at the time of sampling.

All of the population characteristics measured for *Emerita analoga* varied significantly between locations (Table 2). Recruitment as estimated by megalopa abundance varied significantly between beaches (Table 2). Population abundance, and the abundances of ovigerous crabs, overwintered crabs, young of the year crabs and megalopa varied up to more than an order of magnitude between populations. Total biomass varied up to 4 fold and ovigerous biomass up to 16 fold between beaches. Mean individual and mean ovigerous crab mass varied up to 5 fold between beaches. The survival of crabs over the winter to the second season as estimated by the abundance of overwintered female crabs also varied significantly between beaches (Table 2).

Life history characteristics, including the female size at maturity, largest and smallest ovigerous crab size and largest male crab size, varied significantly between beaches (Table 2). That variation was less than observed in other population measures, up to 1.5 fold in length (> 3 fold in weight) between beaches.

The study purposely spanned a restricted geographic range but measures of crab size and life history increased from the western to the eastern beaches while population abundance decreased (Fig. 2abc, 3abc). We found significant correlations between population abundance, mean individual size, female size at maturity, largest and smallest sizes of ovigerous crabs and the coastline distance (Table 3). Population biomass was not correlated with coastline distance.

Once variation associated with coastline distance was removed, some of the life history characteristics were partially correlated with environmental factors (Table 4). Smallest ovigerous crab size and largest male

TABLE 2

Range of mean values and results of one way analysis of variance for *Emerita analoga* populations (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, χ^2 = Kruskal-Wallis test statistic)

Extensión del promedio de valores y resultados de análisis de varianza de una vía para poblaciones de *Emerita analoga*. (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, χ^2 = Kruskal Wallis prueba estadístico)

Population Characteristic	Range	n	F	χ^2
Abundance N m ⁻¹				
All Crabs	1178 - 13517	12	6.09***	
Ovigerous Crabs	64 - 2525	12	16.14***	
Overwintered Crabs	0 - 191	12		22.40**
Young of the Year Crabs	1050 - 13517	12	6.20***	
Megalopa	0 - 573	12		24.71**
Biomass g m ⁻¹				
All crabs	851 - 3504	12	6.00***	
Ovigerous crabs	121 - 1985	12	12.03***	
Crab Size g				
Mean Individual Size	0.14 - 0.72	12	20.37***	
Mean Ovigerous Size	0.37 - 1.94	12	22.56***	
Life History Characteristics mm				
Female Size at Maturity	9.4 - 14.6	12		19.37*
Largest Ovigerous Crab	11.5 - 21.9	12	4.56***	
Smallest Ovigerous Crab	9.4 - 17.7	12		19.73*
Largest Male Crab	8.4 - 14.6	12		29.05**

crab size were partially correlated with surf zone water temperature, sediment diversity and beach slope. Female size at maturity was partially correlated with surf zone water temperature and sediment diversity. Mean ovigerous crab size was partially correlated with sediment diversity.

Aspects of the population biology of *Emerita analoga* were correlated with crab abundance suggesting that intraspecific interactions could influence populations of *Emerita analoga*. Megalopa abundance was positively correlated with population (exclusive of megalopa) abundance ($r = 0.84$, $p < 0.001$). The mean individual size ($r = -0.85$, $p < 0.001$), mean ovigerous size ($r = -0.75$, $p < 0.01$), largest ($r = -0.76$, $p < 0.01$) and smallest ($r = -0.65$, $p < 0.05$) sizes of ovigerous crabs and largest male crab size ($r = -0.64$, $p < 0.05$) were inversely correlated with population abundance.

The sizes of overwintered crabs (largest size of ovigerous crab and the largest male

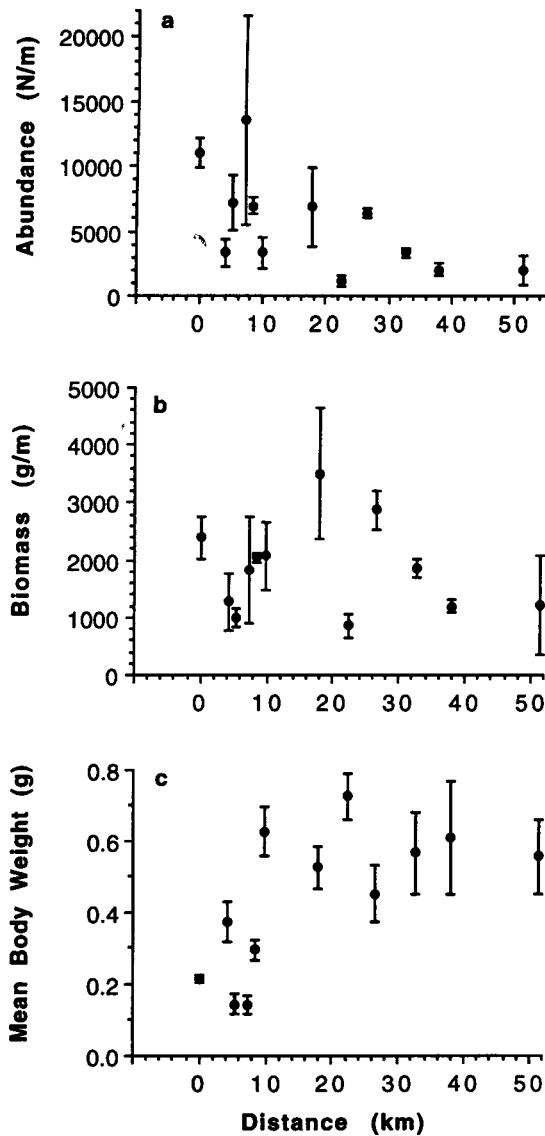


Fig. 2: Means of (a) abundance, (b) biomass and (c) mean individual size of *Emerita analoga* populations as a function of coastline distance from west to east. Error bars represent standard deviations.

Promedios de (a) abundancia, (b) biomasa, y (c) tamaño promedio individual de *Emerita analoga* en función de la distancia costera oeste a este. Las barras corresponden a desviaciones estándar.

crab size) were inversely correlated with megalopa abundance ($r = -0.75$, $p < 0.01$, $r = -0.62$, $p < 0.05$ respectively) indicating that recruitment and survival over the winter may act in opposite ways on the beaches sampled. Mean individual size and mean ovigerous size were also negatively correlated with megalopa abundance ($r = -0.80$, $r =$

-0.70 , $p = 0.01$). Weak negative correlations (nonsignificant) were present between the abundance of overwintered female crabs, and the abundances of young of the year crabs and megalopa.

To examine the potential effect of variation in populations of *Emerita analoga* on

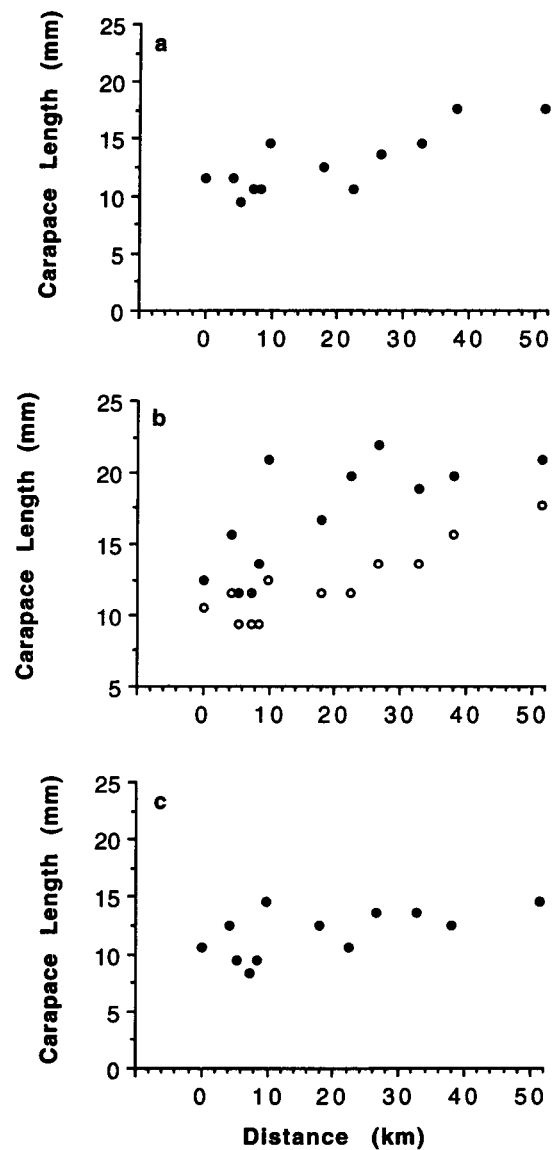


Fig. 3: Means of (a) female size at maturity, (b) largest (closed points) and smallest ovigerous female sizes (open points), and (c) largest male crab size of *Emerita analoga* populations as a function of coastline distance from west to east.

Promedios de (a) dimensión de las hembras en madurez, (b) tamaños de hembras ovígeras más grandes (puntos cerrados) y más chicas (puntos abiertos) y (c) tamaños de los machos más grandes de *Emerita analoga* en función de la distancia costera oeste a este.

TABLE 3

Spearman's rank correlation coefficients for means of population characteristics of *Emerita analoga* and coastline distance (*p < 0.05, n.s. = not significant)

El grado de la coeficiente correlación de Spearman para el promedio de características de población de *E. analoga* y la distancia de la costa (p < 0.05, n. s. = no significativo)

Population Characteristic	Rho (corrected for ties)
Abundance N m ⁻¹	
All Crabs	-0.69*
Ovigerous Crabs	-0.63 n.s.
Overwintered Crabs	0.32 n.s.
Young of the Year Crabs	-0.66*
Megalopa	-0.48 n.s.
Biomass g m ⁻¹	
All crabs	-0.15 n.s.
Ovigerous crabs	-0.15 n.s.
Crab Size g	
Mean Individual Size	0.67*
Mean Ovigerous Size	0.80*
Life History Characteristics mm	
Female Size at Maturity	0.72*
Largest Ovigerous Crab	0.75*
Smallest Ovigerous Crab	0.83*
Largest Male Crab	0.61 n.s.

Emerita analoga are generally greater than predicted for the average macrofauna community at a given beach type. The mean individual size (g) of *Emerita analoga* is generally less than predicted for macrofauna communities. Values for the abundance, biomass and mean individual sizes of *Emerita analoga* populations are more similar to those predicted for communities inhabiting beaches of dissipative morphodynamic type (Dean's parameter ≥ 6) than for beaches of intermediate type.

DISCUSSION

The abundance, biomass, size structure and life history of populations of *Emerita analoga* varied significantly on a local spatial scale. That variation was not correlated with any single environmental factor measured, including an index of beach morphodynamics.

Our results for *Emerita analoga* populations suggest that this species may be relatively independent of beach morphodynamics for intermediate to dissipative beach types. *Emerita analoga* occurred on all but the most reflective beaches and only population biomass increased significantly from reflective to dissipative beaches for 8 populations of *Emerita analoga* inhabiting a narrow latitudinal range in south-central Chile (Jaramillo & McLachlan 1993). Other species of beach macrofauna including cirolanid isopods (Jaramillo & McLachlan 1993) and mesodesmatid bivalves (Dugan & Hubbard un-

community patterns, the means of abundance, biomass and mean individual size of *Emerita analoga* populations from the present study are plotted as a function of Dean's parameter along with macrofauna community trends from around the world (Fig. 4abc). The abundance and biomass of

TABLE 4

Results of multiple linear regressions of means of sand crab population and life history characteristics and environmental variables. (*p < 0.05, **p < 0.01, ***p < 0.001, n.s. = not significant)

Resultados de regresiones línea múltiple de intermedios de características de población e historia de vida para *E. analoga* y variables ambientales. *p < 0.05, **p < 0.01, ***p < 0.001, n. s. = no significativo)

Characteristic	Multiple r	Constant	Distance		Temperature		Sediment Diversity		Beach Slope	
			Coef.	t-stat	Coef.	t-stat	Coef.	t-stat	Coef.	t-stat
Population Abundance	0.74 n.s.	-30563.70	-171.60	2.43*	2048.60	1.05 n.s.	-31156.90	1.38 n.s.	123.80	1.65 n.s.
Population Biomass	0.51 n.s.	6789.50	-2.75	0.14 n.s.	-281.30	0.53 n.s.	1784.20	0.29 n.s.	13.46	0.66 n.s.
Mean Individual Size	0.80 n.s.	1.39	0.01	3.48**	-0.08	0.84 n.s.	1.88	1.78 n.s.	-0.00	1.09 n.s.
Mean Ovigerous Size	0.94**	5.01	0.04	7.11***	-0.28	1.92 n.s.	5.84	3.43*	-0.01	2.06 n.s.
Female Size at Maturity	0.94**	42.12	0.19	6.81***	-1.85	2.45*	29.28	3.36*	-0.06	2.13 n.s.
Largest Ovigerous Crab	0.87*	48.38	0.25	4.55**	-2.18	1.47 n.s.	36.46	2.12 n.s.	-0.03	0.55 n.s.
Smallest Ovigerous Crab	0.98***	42.94	0.17	11.58***	-1.76	4.35**	20.28	4.32**	-0.06	3.57**
Largest Male Crab	0.91**	61.06	0.12	4.93**	-2.73	4.09**	31.02	4.02**	-0.06	2.38*

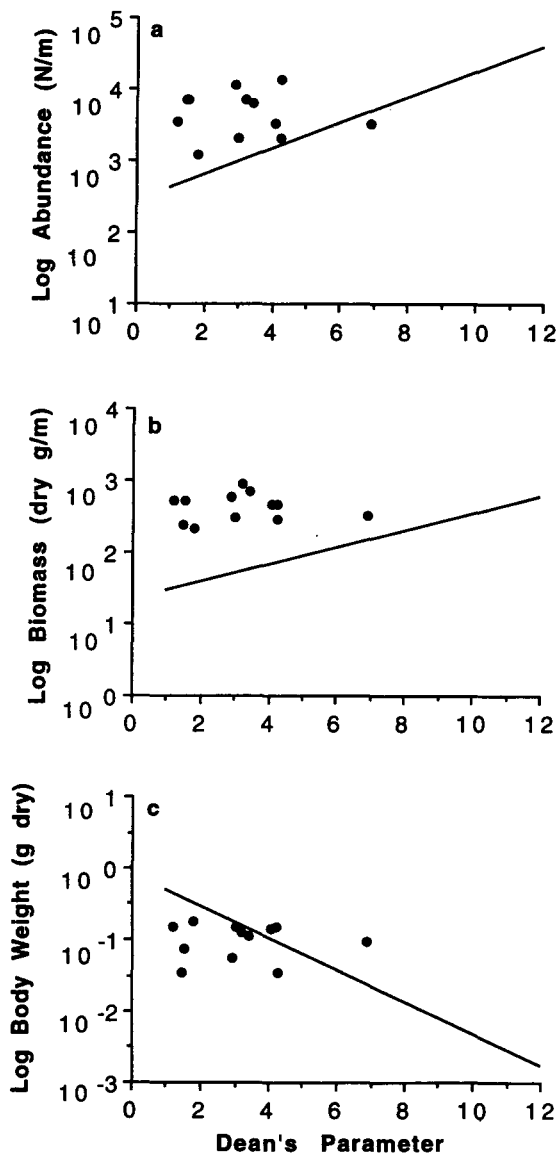


Fig. 4: Means of (a) abundance, (b) biomass, and (c) mean individual size of *Emerita analoga* as a function of beach type (Dean's parameter) in the present study are indicated by points. Regression lines indicate the relationships reported in McLachlan et al. (1993) (ab) and McLachlan (1990) (c) for abundance, biomass and mean individual size of the macrofauna as functions of beach morphodynamic type.

Promedios de (a) abundancia, (b) biomasa, y (c) tamaño promedio individual de *Emerita analoga* en función del tipo de playa (parámetro de Dean), en el presente estudio están indicadas con puntos. Líneas de regresión indican la relación mencionada en McLachlan et al. (1993) (ab) y McLachlan 1990 (c) para abundancia, biomasa y tamaño promedio individual de la macrofauna en función del tipo morfodinámico de la playa.

published) may respond to beach morphodynamics more consistently than *Emerita analoga*. Independence from the influence of beach morphodynamics could contribute to the wide distribution and high success of *Emerita analoga* and other hippids on sandy beaches (e.g. Efford 1976).

Variation in *Emerita analoga* populations associated with location was not completely described by the environmental factors we measured in the present or earlier studies (Dugan et al. 1991, 1994). On a very local scale, variation in the abundance of *Emerita analoga* populations was related to coastline distance alone. However, in agreement with studies on larger geographic scales (Dugan et al. 1991, 1994, Wenner et al. 1993), our results suggest that the size structure and life history of sand crabs on a local scale are also influenced to a lesser extent by a variety of other environmental factors including surf zone water temperature, sediment diversity and beach slope, and population abundance.

Differences between populations of *Emerita analoga* were primarily related to nonenvironmentally explained spatial variation as estimated by coastline distance rather than independent environmental variables (sensu Legendre 1993). Coastline distance may relate to other factors and combinations of factors that could influence populations of this dominant macrofauna species on a local scale. For example, the location of a beach with respect to currents and local hydrography may influence larval supply and recruitment thus affecting population abundance. Studies of the distribution of blue crab, *Callinectes sapidus*, megalopae in Virginia found significant spatial variation in densities of planktonic megalopae on scales of 100's of meters and kilometers but little variability on a 1-2 m scale (Olmi et al. 1990).

Our data suggest that recruitment and survival vary significantly and in opposite directions between populations of *Emerita analoga* inhabiting beaches in the study area. Populations of *Emerita analoga* with high abundances may be the result of high recruitment levels or settlement rates as reported for barnacles on rocky shores by Gaines & Roughgarden (1985). High abundances of megalopa may settle on beaches that are

more exposed to prevailing currents, such as headlands, which could collect larvae from the plankton more effectively than beaches located in bays. The inverse correlations found between megalopa abundance and the size of overwintered crabs suggests that beaches with high levels of recruitment may not be as favorable for growth and survival over winter. The weak negative correlations between the abundance of overwintered female crabs and the abundances of young of the year crabs and megalopa support that idea. Higher abundances of older crabs of larger sizes may occur on beaches where sand is retained through the winter months and survival is higher. Beaches that are more exposed to prevailing currents may experience sand scouring, exposure of underlying rock benches, and less favorable conditions for survival through winter storms.

Our results also suggest that intraspecific interactions can influence populations of *Emerita analoga*. The inverse correlations found between the smallest size of ovigerous crabs and abundance suggest that high abundance may result in decreased growth rates and the attainment of smaller sizes. If smaller crabs have less success overwintering then intraspecific interactions could affect both life history and survival of *Emerita analoga*.

The response or lack of a response of a dominant species to beach morphodynamics and other factors which vary on a local scale can potentially influence community structure. When the abundance, biomass, and mean size of *Emerita analoga* are compared with macrofauna community trends on beaches from around the world, it is clear that variation in this dominant species could potentially influence community patterns in abundance and biomass with respect to beach morphodynamics. *Emerita analoga* composed 4-98% of the biomass and 5-94% of the numbers of individuals of macrofauna in samples from California Channel Island beaches (Dugan et al. in press), 10-39% of the biomass and 1-3% of the abundance of macrofauna on Oregon beaches (McLachlan 1990), and 40-95% of the biomass of macrofauna of beaches in south-central Chile (Jaramillo & McLachlan 1993). Limited indirect evidence of the influence of this dominant species on community patterns is available.

Jaramillo & McLachlan (1993) found the population biomass of *Emerita analoga* and macrofauna community biomass increased significantly from reflective to dissipative beaches while weak trends occurred in abundances for both. The macrofauna communities of sand beaches of California have not been examined with respect to beach morphodynamics, although work by Dugan et al. (in press) suggests that over a range of intermediate beach types, community patterns generally match those described by McLachlan (1990).

Spatial and temporal variation in the abundance and biomass of *Emerita analoga* and other dominant macrofauna species associated with recruitment, fishing pressure and storm events could greatly influence their overall and relative effects on community abundance and biomass. *Emerita analoga* represented a small fraction of the number of individuals on Oregon beaches sampled by McLachlan (1990), and some California Channel Island beaches, while on other island beaches, crab abundances reached 52,000 crabs m^{-1} (Dugan et al. in press). During the spring recruitment period on a California Island beach, densities of *Emerita analoga* were > 13000 crabs m^{-1} , 5 months later, densities averaged 8300 crabs m^{-1} , a 36% decrease (Dugan et al. in press).

Further study of *Emerita analoga* and other dominant species of macrofauna representing a variety of taxonomic groups on appropriate temporal and spatial scales are needed to clarify the role of populations of individual species in generating community patterns observed on sandy beaches. The results of such studies can be used to examine the suggestion of Jaramillo & McLachlan (1993) that community patterns represent a summed response of individual species to physical beach processes and the "autecological hypothesis" (Noy-Meir 1979 as in McLachlan 1990) which states that in physically controlled environments, communities are structured by the independent responses of individual species to the physical environment.

ACKNOWLEDGMENTS

We gratefully acknowledge the generous efforts of E. Jaramillo and his students in

organizing and facilitating a great meeting and editing this proceedings. We thank the participants of "Sandy Beaches '94" for their input and enthusiasm. We thank M. Page and A. Wenner for their support of the field research and comments on the manuscript and M. Hernandez for assistance with translation. This research was supported by a University of Otago postdoctoral fellowship to J. Dugan, the Department of Marine Science at the University of Otago, and the Marine Science Institute at the University of California at Santa Barbara.

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