GROWTH RATE OF THE SAND CRAB, *EMERITA ANALOGA*, (HIPPIDAE) IN TWO DIFFERENT ENVIRONMENTS

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ABSTRACT

The field growth rate of *Emerita analoga* was estimated under two different sets of environmental conditions. One beach location on the southern California coastline near Santa Barbara was compared with a beach on Santa Cruz Island, only 42 km distant. The island population of *E. analoga* experienced colder water which contained less suspended solids than the mainland population studied. The crabs on the island beach were found to grow at about one-third the rate of those on the mainland, as measured by the "instantaneous growth rate" technique.

The growth rate of a crustacean species is of considerable ecological interest for at least two reasons. First, the usual positive relationship between body size and fecundity means that an increased growth rate may increase reproductive output. Second, the proportion of animals which are mature within any specified population will depend on the growth rate (to maturity) of its members. These relationships indicate that a measure of individual growth, averaged for a population, may give information about reproductive success and, therefore, about the persistence of a population under its particular set of environmental circumstances. Further, comparison of the growth rates for populations of the same species under differing environmental regimes may indicate how the species responds to its environmental conditions in terms of growth.

The proximity of the Channel Islands to the mainland near Santa Barbara provides excellent opportunity for comparative studies. The differing oceanographic conditions between some beaches of Santa Cruz Island and nearby Goleta Bay on the mainland allow an analysis of growth as a function of different environmental characteristics. This is the intent of the present work.

This study is an analysis of the growth rate in two nearby populations of the sand crab, *Emerita analoga*. It is an anomuran crab which inhabits beaches of the eastern North Pacific from southern Canada to central Baja California. There also are populations of the species in the Gulf of California and the eastern South Pacific, but these populations are not considered here. The crab normally lives between high and low tide marks buried in sand on sandy beaches, and follows the water's edge up and down the beach with the tides. The crab is somewhat unusual for its family in that it procures its food by filtering seawater that washes over its finely setose second antennae as waves rush onto and ebb from the beach face. *Emerita analoga* can often be found in dense aggregations on beaches of southern California during spring and summer. This species was chosen for comparative growth study because: 1) it is seasonally very abundant and easily captured in great numbers; 2) it is of a size which facilitates the handling and treatment of such numbers; and 3) it inhabits beaches of the mainland and beaches on nearby Santa Cruz Island.

Several methods have been used in the past to measure the incremental type of growth experienced by crustaceans, all of which have merits and drawbacks. These methods include: field caging, laboratory confinement, mark and recapture methods, and modal size class analysis. The best of these for the estimation of field growth rate is field caging. This method, unfortunately, cannot be applied to sand crabs living in their shifting sand habitat. For reasons presented in detail in the methods, a different approach has been used to measure growth for *E. analoga* The "instantaneous growth rate" method used here takes advantage of certain aspects of the crustacean molt cycle to minimize handling effects while estimating field growth rate. Both molt increment and molt frequency measures are taken, which are combined to give an instantaneous growth rate for an average individual of each population. By this method the response of growth to different en-

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vironmental conditions in the field can be observed for this species.

METHODS

Several alternatives for the measurement of growth for *Emerita analoga* were possible, including all those mentioned above. Field caging did not seem practical, and laboratory impoundment does not provide information on the growth rate in the field situation. Mark and recapture techniques are adaptable to the species (Dillery and Knapp 1970), but considerable time and effort can be expended for very little data return. The usual recapture rate is low, 10% or so at best, unless unusual circumstances, e.g., a fishery, exist. Modal size class analysis can give an index of average growth, but can be misleading without corroborative evidence from the laboratory or some other method of growth measurement. Unfortunately, no such corroborative data exist for *E. analoga*. As a result of these considerations, an instantaneous growth rate method was chosen to estimate growth for this species. This method as applied to *E. analoga* is described in the following sections.

Localities

Two locations were chosen on the basis of their proximity and on preliminary observed differences in their environmental conditions. One site, the beach of Goleta Bay adjacent to the University of California Santa Barbara campus, is bathed in relatively warm water (mean surface temperature for 1974 and 1975: 13.7°C) that is relatively turbid (average lateral visibility: <1 m).

The second site, a bay on the northwest corner of Santa Cruz Island, is about 42 km (25 mi) south of the coast of Santa Barbara, and experiences much different water conditions. At this location, water clarity is almost always excellent (10-20 m of lateral visibility), indicating a relative lack of suspended materials. In addition, Neushul et al. (1967) described current patterns in the vicinity which indicate that this site is bathed in a colder water mass originating in the north. The mean surface temperature measured at the Santa Cruz Island site during 1974 and 1975 was 12.1°C.

Sampling

Sand crabs were gathered and separated into size classes by methods described fully in Wenner et al. (1974). The use of an automatic size sorting sieve permitted measurement of a large number of live crabs rapidly. Samples were taken approximately biweekly at Santa Cruz Island and Goleta in 1974 and monthly at Goleta in 1975. The crabs, separated into size classes, were then placed in screen compartments in sand in a continuous flow seawater table for a period of 5 days. Every day each compartment was checked for molts, and the number of molts and molt increments were recorded. Where multiple molts occurred in any size class on 1 day, premolt and postmolt carapace length were paired by rank from least to greatest measure. This procedure might tend to reduce the variance in molt increment slightly, but no significant differences were found between single molt and multiple molt records for 20 molt increment observations during May-July at Goleta in 1974 ($0.5<P<0.6$, $t = 0.667$, df = 36).

Water temperature data were taken at the time of sampling, and water temperature was monitored throughout the 5-day holding period. Water samples were also taken monthly from July to October 1975. The water was filtered through preashed, preweighed Whatman[2] GF-C glass fiber filter paper under 4-5 lb vacuum, after coarse filtration through a 2-mm screen. Efford (1966) suggested that *E. analoga* can handle particles between 5 μm and 2 mm. The filter paper filtered particles down to approximately 5 μm in size. Thus an approximation of the range of particle sizes utilized by *E. analoga* was filtered from the water. Filterable solids (grams/liter) were measured in this way from both sites.

Instantaneous Growth Rate Rationale

Given that two parameters of crustacean growth, i.e., molt increment and molt frequency, are the factors which need be estimated, a method is required which minimizes handling effects but which still allows observation of size-specific changes in these measures.

Prolonged impoundment in a laboratory situation tends to affect both the molt increment and molt frequency; however, aspects of the crustacean molt cycle provide an advantage if crabs are held in the laboratory for a short period of time. Drach (1939) described the molt cycle of *Cancer*

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

pagurus. From this description it is clear that a crustacean actually spends a great deal of its time involved with the molting process. Once the specific stimulus to molt has occurred, environmental changes seem to have little effect in modifying the process (Green and Neff 1972). In other words, a crab which is about to molt will molt. In fact, keeping *E. analoga* in running seawater tables for a very short portion of their molt cycle does not alter a relatively high value for molt frequency and increment. For example, Table 1 shows data from a 14-day period in which *E. analoga* were kept in running seawater tables. These data suggest that for a period of 5 days or so *E. analoga* may be relatively unaffected by impoundment in running seawater tables, but that confinement for longer periods reduces both the increment at molt and molt frequency.

From the above, it follows that keeping *E. analoga* in running ambient seawater tables for a period of 5 days generates relatively accurate "instantaneous" estimates of field growth rate for these crabs. This allowed me to collect sand crabs from the field, place them in seawater tables within 2 or 3 h after collection, and monitor them daily. Molt increment was measured directly as animals within each size class molted, and molt frequency was calculated by the formula: $f_m = t/p_t$ where f_m = molt frequency in days, t = total number of days held, and p_t = proportion of animals which molted in t days. For instance, if half the crabs molted in 5 days, the average molt frequency would be 10 days.

TABLE 1.—Molt records for *Emerita analoga* kept in running seawater tables for 14 consecutive days.

Day	Total no. molts from 264 crabs	$\bar{x}$ molt increment[1]	Day	Total no. molts from 264 crabs	$\bar{x}$ molt increment[1]
1	13	1.2	8	4	0.8
2	11	1.3	9	8	0.9
3	19	1.2	10	6	—
4	27	1.0	11	5	—
5	17	1.2	12	2	—
6	9	0.8	13	3	—
7	7	0.9	14	2	—

[1] At 5.9 mm premolt carapace length.

RESULTS

Environmental Differences

Water temperature showed a consistent annual difference between Goleta Bay and Santa Cruz Island for 1974 and 1975 (Figure 1), though the peak water temperature for 1975 was the same for both locations. During June-October 1974, the mean surface temperature difference between sites was 2.9°C. Peak water temperature was maintained for about 2 mo (mid-June to mid-August) at Goleta Bay in 1974 while Santa Cruz Island experienced peak temperature for a month or less.

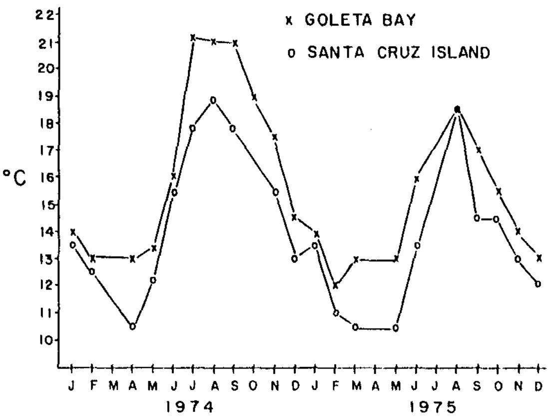

FIGURE 1.—Annual surface temperature variation at Goleta Bay and the western tip of Santa Cruz Island for several years. Data from March to October 1974 are from direct observation. All other data are from U.S. Coast Guard sea surface isotherm charts for Point Conception south.

Four water samples, taken at each location monthly between July and October 1975, showed a large significant difference ($P < 0.001$, t = 6.36, df = 14) between the amount of filterable solids in the water washing onto the two beaches. Goleta Bay averaged 0.11321 ± 0.02933 g/l of filterable solids while Santa Cruz Island averaged 0.04416 ± 0.00925 g/l. This means that about 2½ times as much filterable material was potentially available for *E. analoga* at Goleta Bay as at Santa Cruz Island. Unfortunately, organic content of these samples was not measured. This would have been a more reliable index of food availability than filterable solids.

Growth

Comparison of data from Goleta Bay in 1974 and 1975 indicates that the instantaneous growth rate method produces repeatable results and that the growth rates at Goleta Bay for the two time periods were about the same (Table 2). Comparison of data from Goleta Bay and Santa Cruz Island in 1974 indicates that sand crabs from the island site were molting about half as often, on the average, as those crabs from Goleta Bay during the

TABLE 2.—Summarized growth data for sand crabs from Goleta Bay and Santa Cruz Island in 1974 and 1975. Mean ± SD is given for each measure.

Item	Goleta Bay		Santa Cruz Island, 1974		
	1974	1975	All samples	First 3	Last 3
Molt increment (mm):					
Sample size	581	629	188	118	70
$\bar{x}$ increment	0.9 ± 0.3	1.0 ± 0.4	0.6 ± 0.3	0.8 ± 0.3	0.4 ± 0.2
$\bar{x}$ premolt carapace length	7.3 ± 1.8	7.4 ± 4.2	7.5 ± 2.7	8.0 ± 3.0	7.4 ± 1.8
Molt frequency (days):					
Sample size	1,785	1,334	1,703	717	986
$\bar{x}$ frequency	26 ± 19	18 ± 11	50 ± 24	36 ± 18	63 ± 22
$\bar{x}$ premolt carapace length	7.7 ± 1.8	7.0 ± 3.4	7.7 ± 3.1	8.8 ± 3.5	7.0 ± 1.6

sampling period. Also, the island site crabs gained about a third less in carapace length at each molt than the mainland animals (Table 2). Thus, sand crabs at the island beach would take about three times as long as the Goleta Bay crabs to reach a given size, growing at the observed rates. Calculation of the instantaneous rate of growth (molt increment ÷ intermolt period) for the two beaches in 1974 gives values of 0.035 mm/day for Goleta Bay and 0.012 mm/day for Santa Cruz Island

Separation of the Santa Cruz Island samples into two equal time periods (May-early July, late July-September) yielded an interesting observation. The later group of samples showed a much lower growth rate than did the earlier, which can be explained by the steady decline in molt increment (Figure 2). The relatively high value (0.9 mm) in late May could represent a peak, but the island site was not sampled prior to May. The pattern of molt increment vs. time for Goleta Bay (Figure 2) was different, showing peaks in July and September. The decrease in August may reflect changes in the number of maximum size males, which decrease in molt increment as they approach maximum size, and also may reflect an influx of juvenile crabs into the population in August. The first peak corresponds in time with the peak water temperature for the sample period (Figure 1). This may be a result of a physiological response to temperature by *E. analoga*. Crabs observed in the laboratory at different temperatures fed at different rates. Those in warmer water fed most often (Fusaro 1977).

At both locations, molt increment was positively correlated with size (Figure 3). The difference between means of molt increment from the two locations was 0.3 mm, amounting to about one-half of an average molt increment for the Santa Cruz Island beach population.

Molt frequency data could not be correlated with carapace length at either location, although a generally similar trend existed in most samples. A

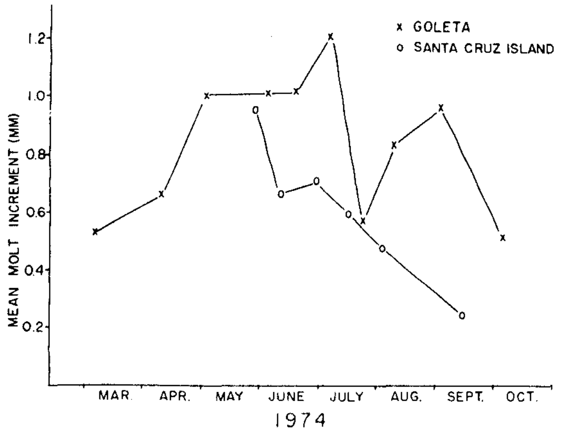

FIGURE 2.—Molt increment vs. time for sand crabs from Goleta Bay and Santa Cruz Island. Each point is a mean for that sample date.

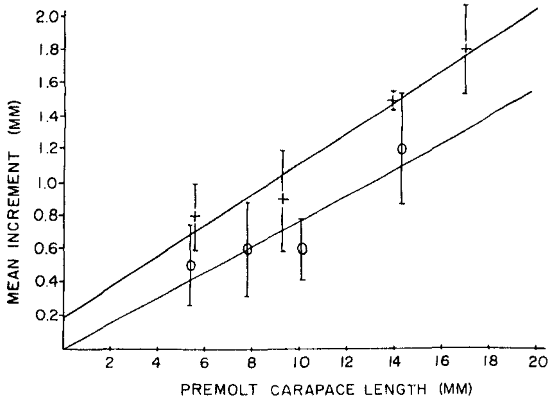

FIGURE 3.—Regression of mean molt increment on premolt carapace length for grouped size class data of sand crabs from Goleta Bay (+'s) and from Santa Cruz Island (0's). Regression line equations are $Y = 0.0932X + 0.1829$ for Goleta Bay and $Y = 0.0776X - 0.0041$ for Santa Cruz Island. Correlation coefficients are 0.98 for Goleta Bay and 0.92 for Santa Cruz Island. Vertical bars at each point represent ± 1 SD.

relatively high molt frequency was observed at smaller sizes (about every 7-12 days/molt at 5 mm carapace length), and this value increased generally in larger size classes (to about every 80-90 days/molt at 20 mm carapace length). Molt frequency averaged over a similar range of premolt carapace lengths did reveal, however, a large difference between the populations on the two different beaches (Table 2).

Population structure data reveal differences in several measures which relate to the growth rate of *E. analoga* (Table 3). The mean size of both males and females was reduced at the Santa Cruz Island site. The proportion of females larger than the mean minimum size of ovigerous females was drastically reduced at the Santa Cruz Island site (2.7% compared with 21.1% at Goleta). In addition, the overall proportion of females which were ovigerous was much smaller at the island site (1.1% compared with 19.4% at Goleta).

TABLE 3.—Population structure data from pooled samples of *Emerita analoga* between June and September 1974. All size values are in millimeters carapace length and sample sizes are in parentheses.

Item	Goleta Bay	Santa Cruz Island
Mean size ♂	7.5 (8,956)	6.0 (6,951)
Mean size ♀	9.7 (6,347)	7.5 (7,730)
Mean % ovigerous ♀	19.4 (6,347)	1.1 (7,730)
Mean min size ovigerous ♀	13.8 (6,347)	13.8 (7,730)
% ♀ >13.8 mm carapace length	21.1 (6,347)	2.7 (7,730)

DISCUSSION

Methods for Measuring Growth

The growth rate of crustaceans in nature, though of considerable research interest, has been difficult to measure for several reasons. Primarily, all of the hard parts of the animal are cast off with the molt, making the marking of them all but impossible until recent years. Wenner et al. (1974) discussed the problems associated with measuring growth for crustaceans, and their table 1 summarized possible patterns of growth for the Crustacea. That table stressed the relative contribution of two factors in crustacean growth: molt increment and molt frequency. Both of these may be responsive to different environmental parameters, altering the growth pattern of a species.

The standard methods for measuring field growth rate for crustaceans (caging, mark and recapture, and analysis of modal size classes without corroborative data) are unsatisfactory to compare field growth rates for different populations of *E. analoga*. Since none of these methods alone suffices for this kind of comparative measurement with *E. analoga*, the instantaneous growth rate approach was used in this comparative analysis. The method has qualities common to some of the other methods mentioned, but avoids some of the inherent problems of those methods. This technique allows direct observation of size-specific molt frequency and molt increment, while minimizing the handling effects normally associated with laboratory impoundment. It is likely that molt frequency estimates by this method are more accurate for the larger crabs, for which the 5-day holding period is a relatively smaller proportion of the intermolt period. The method has allowed comparison of growth factors (molt increment and frequency) in detail for *E. analoga* and gave repeatable data such as that found for Goleta Bay in 1974 and 1975. Thus a technique for measurement of crustacean growth has been developed here which may hold promise for such comparative studies as this, where field caging is impractical.

Growth of *Emerita analoga*

The large difference in the growth rate of *E. analoga* between beaches of Goleta Bay and a Santa Cruz Island bay is remarkable in view of their proximity (about 42 km apart) but not in view of the different environmental conditions found at each beach. The combination of colder water and reduced filterable material in suspension in the water appears to have slowed the growth of *E. analoga* on Santa Cruz Island. This difference is evidence of the sensitivity of these two factors of sand crab growth to variation in environmental qualities.

It is tempting to construct growth curves from such data on molt increment and molt frequency, having arrived at estimates for these. Both of these factors, however, have been shown to be highly responsive to environmental conditions. In fact, they vary widely in time and space with no clear pattern emerging as yet. A growth curve constructed from these data would apply only under a specific set of environmental conditions. Certainly these large differences in growth rate in nearby beaches precludes the use of modal size classes from several beaches for the determination of growth for *E. analoga*, as Efford (1967) did earlier.

Efford (1967:84, figure 3) presented a growth curve for *E. analoga,* constructed from data taken from 22 beaches on the Pacific coast between Ensenada, Mexico, and Tofino, Canada (a 2,400 km distance). Three-fourths of the data presented were gathered over a period of only 2 mo (between 17 June and 17 August 1961). The remaining data were collected in 1959 and 1963. Where size-frequency data were bimodal, the author assumed that two year classes were present. To construct a growth curve from his data, Efford also had to assume that: 1) growth rate was the same year to year (temporally stable, at least during the growing season); and 2) longshore migration did not take place for *E. analoga.*

Dillery and Knapp (1970) demonstrated that an average *E. analoga* individual of about 26 mm carapace length travels about 15 m/day alongshore in an easterly direction on local beaches in Santa Barbara. This implies that the individuals in inhabiting a particular location may change from day to day. Barnes and Wenner (1968) suggested that the interpretation of size-frequency data is considerably simplified if sex reversal is assumed for this species, and some direct evidence (Wenner 1972) supports this assumption. However, recent laboratory data (Fusaro 1977) suggest that a differential growth rate for males and females between 9 and 14 mm carapace length may account for the observed size-frequency distributions and sex ratio patterns, rather than protrandry.

Combining data from different beaches, as Efford (1967) did, also carries with it the assumption that the growth rate is relatively the same for the various parts of the range of *E. analoga* (spatially stable). However, in an analysis of *E. talpoida* data presented by Wharton (1942), Efford suggested that the growth pattern of this latter species may differ in the southern part of its range. It is likely that temperature was responsible for the difference, as it is likely that temperature has an effect on the growth of *E. analoga* in different parts of its Pacific coast range.

Wenner et al. (1974) presented data (their figure 5) which suggested that for *E. analoga,* even different local populations may display different growth patterns, at least as indicated by size at sexual maturity. Data presented in this report imply that molt increment and molt frequency are indeed different in different environmental regimes in nature. Growth curves constructed for such different areas would likely differ. To combine these sets of data would be to obscure the real differences in growth rate observable in such local, proximate populations.

The instantaneous growth rate estimate, though, may be used as an index of how well a population fares under a given set of environmental conditions. Consider this instance. It has been shown that a population of *E. analoga* on a beach at Santa Cruz Island grew about one-third as fast as a population in Goleta Bay (molt increment depressed by one-third and molt frequency depressed by one-half). Assuming a fixed number of molts to maturity (e.g., Wenner et al. 1974, table 1), the island population would reach maturity at a smaller size and in about twice as long a time. In fact, population structure data (Table 3) shows that sand crabs from the island population reached maturity at about the same size as those from Goleta Bay. If a fixed size at maturity is assumed, the island population sampled would take about three times as long to reach that fixed size.

The third possible assumption, that there is a fixed length of time to maturity, is argued against by all available data. In any of these cases, however, the population of sand crabs inhabiting the beach of the Santa Cruz Island bay location was at a distinct disadvantage in terms of reproductive success when compared with the population of *E. analoga* inhabiting the Goleta Bay beach. This reproductive disadvantage was brought about at least in part by the large observed differences in molt frequency and molt increment at the two locations. A much smaller percentage of females were of reproductive size, probably due to the differential growth rate (see Table 3).

Cox and Dudley (1968) also reported large variations in the size of the smallest egg bearing female *E. analoga* found in their collections. Data presented here may account for such previously problematical observations, in that differences in growth rate may affect the size distribution and abundance of mature females.

As these data suggest, then, the growth rate of a crustacean population plays an important role in the life history of that species in its particular environmental situation. Of course, when dealing with a species which has pelagic larval stages, it becomes difficult to study local populations under the assumption that they are genetically different. Recruitment patterns are not generally well known for species with pelagic larvae (see Thorson 1950; Efford 1970; Mileikovsky 1971; Strathmann

1974), thus confounding the issue of reproductive success for a population in a particular habitat. Thus "relative reproductive success" may not be as good a criterion between populations such as these as it is between species. Measurement of differences in such life history factors as growth rate may, therefore, take on added significance in the comparison of two populations or species in differing environments, inasmuch as they do not depend on the assumption of genetic isolation but concern themselves more with the relationship of the population to its particular environmental circumstances.

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