

EGG PRODUCTION BY SAND CRABS (*EMERITA ANALOGA*) AS A FUNCTION OF SIZE AND YEAR CLASS (DECAPODA, HIPPIDAE)

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ABSTRACT

The relationship between egg number, size, and year class was determined for sand crabs (*Emerita analoga*) collected at three California sites, including two different dates for two of those sites. Size frequency distributions of sand crab population samples collected in 1982 from San Clemente, Goleta (2 dates), and Pismo Beach (2 dates) were separated into three modal size/year classes before plotting the size and egg number data and calculating regressions for egg number as a function of size. The slope of the regressions for within year class data generally decreased with increase in age. Both seasonal and locality differences were found in comparisons of data for individual year classes. The technique can be used to compare egg production between female crabs of similar ages between sites and/or dates.

INTRODUCTION

Female crustaceans generally produce more eggs as they grow larger (*e.g.*, Barnes and Barnes, 1968; Van Dolah and Bird, 1980; Hartnoll, 1985). Other animals with indeterminate growth, such as fish (*e.g.*, DeMartini and Fountain, 1961; Bagenal, 1967; Macgregor, 1968; Moe, 1969; Dietrich, 1979; Hunter and Macewicz, 1980; Love and Westphal, 1981; Baltz and Knight, 1983; see also the earlier listing in Altman and Dittmer, 1972), also produce greater numbers of eggs as they grow larger.

The fact that eggs are brooded externally and are thus visible in most crustaceans has led to a considerable amount of research on size-related egg production in that group (*e.g.*, isopods, Paris and Pitelka, 1962, and Lawlor, 1976a, b; mysids, Mauchline, 1973; prawns, Wickens and Beard, 1974; fairy shrimps, Daborn, 1975; barnacles, Barnes and Barnes, 1968, and Hines, 1976; amphipods, Von Dolah and Bird, 1980; hermit crabs, Bertness, 1981; lobsters, Ennis, 1981; krill, Denys and McWhinnie, 1982; brachyurans, Hines, 1982; copepods, Carter *et al.*, 1983; and tanner crabs, Somerton and Meyers, 1983).

Egg production by hippid crabs, which are easily collected and occur throughout the world (Efford, 1976), has received much attention (*e.g.*, Osorio *et al.*, 1967; Efford, 1969; Eickstaedt, 1969; Subramoniam, 1977, 1979; Diaz, 1980). Estimates of hippid egg production have usually been done as a part of life history studies.

While studying reproductive patterns of the common sand crab (*Emerita analoga*) living near a power plant (*e.g.*, Auyong, 1981; Siegel and Wenner, 1984), it became apparent that the overall reproductive output of a population might be impaired if sand crabs were under environmental stress. However, the published data

on *E. analoga* egg production were not sufficient for estimating reproductive output and were frequently inconsistent (*e.g.*, see Eickstaedt, 1969, and Efford, 1969).

The present report summarizes the results of a study of the relationship between size, age, and egg production in three geographically separated populations of the common sand crab at different times during the reproductive season, as clarified by a modal size class (year class) analysis (*e.g.*, Harding, 1949; Cassie, 1954; Wenner and Fusaro, 1979).

MATERIALS AND METHODS

The analysis of egg production and size/year class relationships was based upon ovigerous sand crabs of all available sizes collected in 1982 from each of three California locations, two of which were in the Southern California Bight (San Clemente and Goleta). Fifty-nine ovigerous crabs were collected on 3 August 1982 from San Clemente State Park beach. Two collections were made at Goleta Beach Park; on 25 August 1982, 83 ovigerous crabs were collected, and on 13 October (49 days later, at the end of the reproductive season) 52 more crabs were collected in that area. Two collections were also made at the Pismo Beach pier, on 17 May 1982 (51 ovigerous crabs) and 119 days later on 13 September (25 crabs).

Crabs were initially measured with a graded sieve (Wenner *et al.*, 1974) to the nearest 0.5 mm carapace length (if less than 17.5 mm CL) or to the nearest 1 mm CL (if more than 17.5 mm CL). The size frequency distribution data for all female crabs (ovigerous and non-ovigerous) were then separated into component modal groups (*e.g.*, Harding, 1949; Cassie, 1954; Wenner and Fusaro, 1979; Siegel and Wenner, 1985). The use of probability graph paper for breaking size frequency distributions into constituent modal size/year classes is appropriate because sand crab laboratory growth rates were correlated with year class modes obtained by analyses of changes in field population structure through time (Siegel and Wenner, 1985).

When possible, 5 crabs with newly extruded eggs (stages 2–4 of Boolootian *et al.*, 1959; Eickstaedt, 1969) were chosen for egg counts from each of the 0.5 or 1.0 mm size classes. Crabs with eggs still attached were preserved in a mixture of 30% seawater, 30% ethanol, 30% acetone, and 10% glycerol, a mixture in which the egg diameters remained constant until counting.

Prior to estimating egg number, each preserved crab was measured with calipers to the nearest 0.05 mm carapace length (CL) and washed gently in fresh seawater. Eggs were then removed from the pleopods, checked under the microscope for developmental stage, examined for parasite presence, and placed in an open-ended pipette with a 250 μ nylon screen glued to the bottom to permit water displacement. Known numbers of eggs added to the submerged pipette permitted calculation of a calibration curve, allowing egg number to be estimated by volume in a technique similar to that used by Diaz *et al.* (1983). Eggs were counted directly if they numbered fewer than 1000.

Data points were first ascribed to the appropriate size/year class, after determination by prior modal size class analysis. The data were then plotted in semi-log transformation to obtain regressions for egg number as a function of size. The sizes of crabs within year classes were compared between sites using one-way ANOVA and Tukey-type multiple comparison tests. ANCOVA was not used, because it was not appropriate for the entire data set due to the fact that the year classes, after separation, had non-overlapping ranges for the covariate size. The relationship between size and egg number was compared between year classes at each site and date with multiple comparison of slopes, by use of a Tukey-type comparison (Zar, 1984).

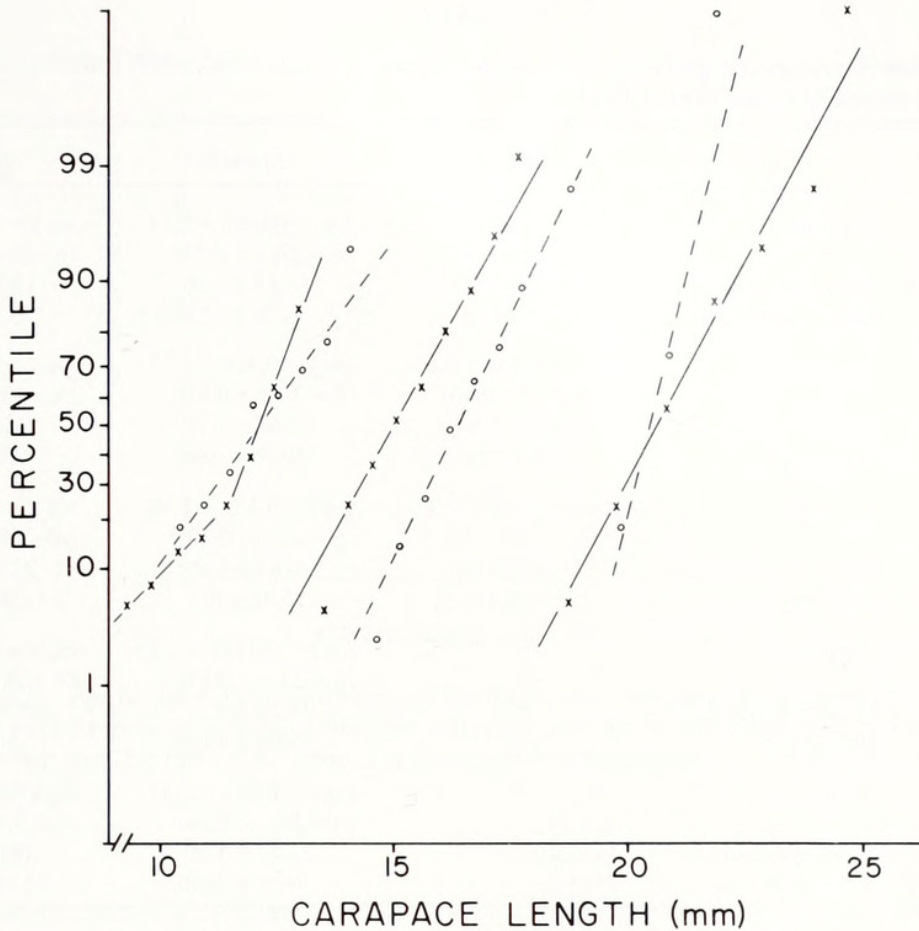


FIGURE 1. Modal size class breakdown for sand crab population structure in 1982 at San Clemente on 3 August 1982 (open circles) and at Goleta on 25 August 1982 (×).

RESULTS

Modal size class analysis and egg number

The modal size class analysis of the frequency distributions yielded similar results for Goleta and San Clemente (the two sampling sites in the Southern California Bight), with three distinct year classes apparent at each location (Fig. 1; see also Siegel and Wenner, 1985). The overall pattern of egg number as a function of size at those two sites was also similar for the first two year classes (Figs. 2, 3; Table I), but egg production by the few third year crabs which were found at San Clemente was highly variable.

The slope of the line depicting egg number as a function of size was quite steep for first year and less so for second year crabs from the San Clemente sample. Since third year ovigerous crabs were scarce and the egg numbers highly variable (Fig. 2), the regression line for that mode was omitted from the figure (included in Table I).

The regression of the 25 August Goleta data for egg number as a function of size for each year class yielded three corresponding lines with their slopes again decreasing with age and size (Fig. 3; Table I). The egg number data for third year Goleta crabs were tightly clustered and consistent compared to the high scatter in egg number for third year crabs from the San Clemente site.

Whereas a high percentage of first year crabs produced eggs at both southern sites, only one first year ovigerous crab was found in the 13 September Pismo Beach sample

TABLE I

Size and egg number relationships for modal size/age classes of female sand crabs (Emerita analoga) collected from three California sites in 1982

		Mode I	Mode II	Mode III
San Clemente (3 Aug.)	Formulas	$\log y = 0.19x + 0.49$ ($n = 24$; $r = 0.85$)	$\log y = 0.09x + 2.14$ ($n = 29$; $r = 0.77$)	$\log y = 0.12x + 1.23$ ($n = 6$; $r = 0.56$)
	Mean size (mm CL)	13.09 ± 1.03	16.85 ± 1.20	19.88 ± 0.97
	Mean egg # ($\pm$ SD)	1193 ± 626	4128 ± 1237	4782 ± 2149
Goleta (25 Aug.)	Formulas	$\log y = 0.20x + 0.62$ ($n = 25$; $r = 0.90$)	$\log y = 0.12x + 1.65$ ($n = 38$; $r = 0.87$)	$\log y = 0.04x + 3.01$ ($n = 20$; $r = 0.73$)
	Mean size (mm CL)	12.17 ± 0.91	15.64 ± 1.16	20.40 ± 1.43
	Mean egg #	1109 ± 449	3069 ± 1036	6808 ± 1216
Goleta (13 Oct.)	Formulas	$\log y = 0.04x + 0.13$ ($n = 13$; $r = 0.10$)	$\log y = 0.12x + 1.19$ ($n = 25$; $r = 0.48$)	$\log y = 0.05x + 2.46$ ($n = 14$; $r = 0.33$)
	Mean size (mm CL)	13.38 ± 0.68	16.64 ± 0.90	22.00 ± 1.35
	Mean egg #	567 ± 317	1510 ± 703	$11,900 \pm 3650$
Pismo (17 May)	Formulas		$\log y = 0.074x + 2.23$ ($n = 23$; $r = 0.83$)	$\log y = 0.06x + 2.44$ ($n = 28$; $r = 0.69$)
	Mean size (mm CL)		21.23 ± 1.77	27.93 ± 1.55
	Mean egg #		4400 ± 1450	$11,900 \pm 3650$
Pismo (13 Sept.)	Formulas		$\log y = 0.07x + 2.35$ ($n = 19$; $r = 0.76$)	$\log y = 0.02x + 3.67$ ($n = 5$; $r = 0.34$)
	Mean size (mm CL)	17.2 mm	23.47 ± 1.40	29.02 ± 1.48
	Mean egg #	1513	9600 ± 2490	$17,160 \pm 3350$

(Fig. 4; Table I). Pismo Beach crabs in the second and third year classes produced considerably more eggs than those crabs in the same year classes from Goleta (25 August) and San Clemente (3 August) beaches. (The modal size class separation for crabs collected on 17 May from Pismo Beach appears in Siegel and Wenner, 1985; the three year class modes were very distinct at Pismo Beach.) The size range and egg production values obtained for second and third year crabs at Pismo Beach essentially did not overlap data for second and third year crabs either from San Clemente or from Goleta Beach.

Within each year class the ovigerous female crabs were different in size at Pismo (September), Goleta (August), and San Clemente (ANOVA: year 1, $P < 0.0014$, year 2, $P < 0.001$, year 3, $P < 0.001$). The differences were statistically significant in all comparisons (Tukey multiple comparisons: $P < 0.001$), except in the comparison of third year female crabs for Goleta (August) and San Clemente (n.s.). (The data for egg numbers were not compared between sites for each of the year classes in this study due to the appreciable size differences found; see methods.)

Comparisons of the slopes of the regressions of size and egg number for each year class at each sampling date and site revealed significant differences in slope between year classes for first and second year female crabs at San Clemente ($P < 0.005$) and all three year classes in August at Goleta ($P < 0.001$). All other slope comparisons yielded differences that were not significant.

The difference in mean size of crabs in the equivalent year class modes, both between year classes at the same time of year and between collecting dates in 1982, agreed with earlier results gathered with respect to the amount of growth expected for a year class mode within the season and between years (e.g., Siegel and Wenner, 1985).

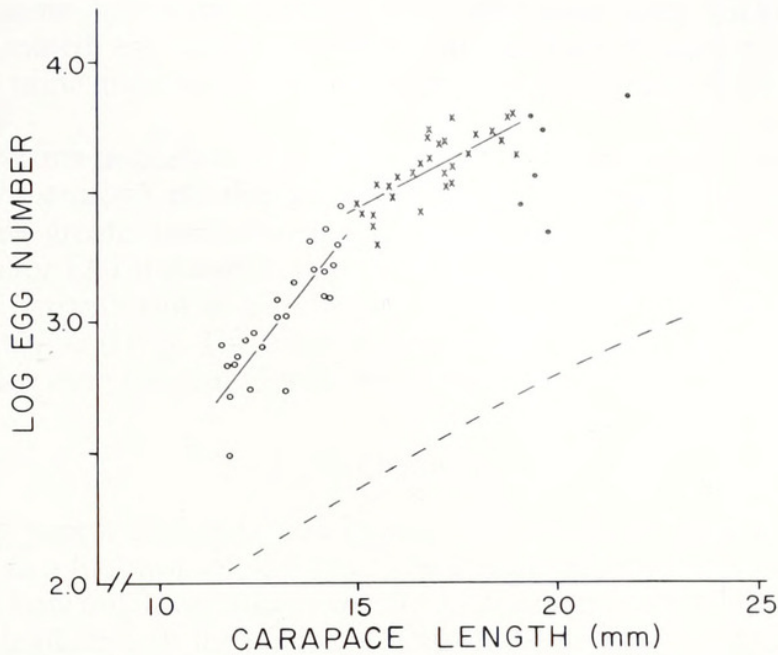


FIGURE 2. Egg production as a function of size for the San Clemente State Beach sample of 3 August 1982. Open circles represent first year crabs, the $\times$ marked individuals are second year crabs, and the closed circles represent data for third year crabs. The broken line was extracted from a plot published by Efford (1969); see text.

The mean number of eggs produced within each year class decreased between the two sampling dates (25 August and 13 October) for Goleta crabs (Table I, Student's t -test; $P < 0.001$), despite the significantly larger mean size of female crabs in the

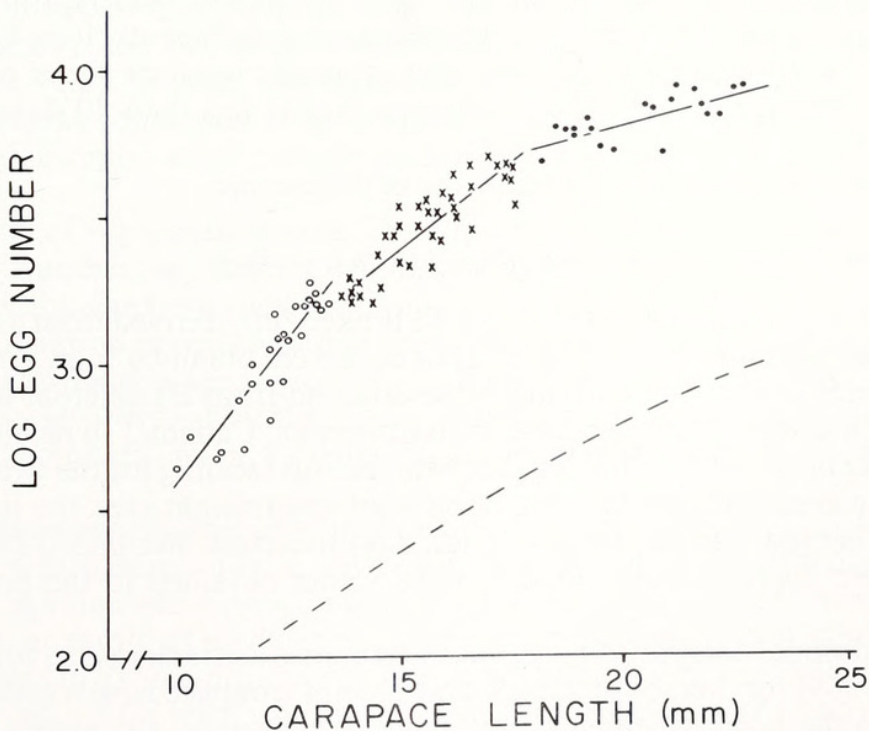


FIGURE 3. Egg production as a function of size for Goleta sand crabs on 25 August 1982. Symbols and broken line are the same as for Figure 2.

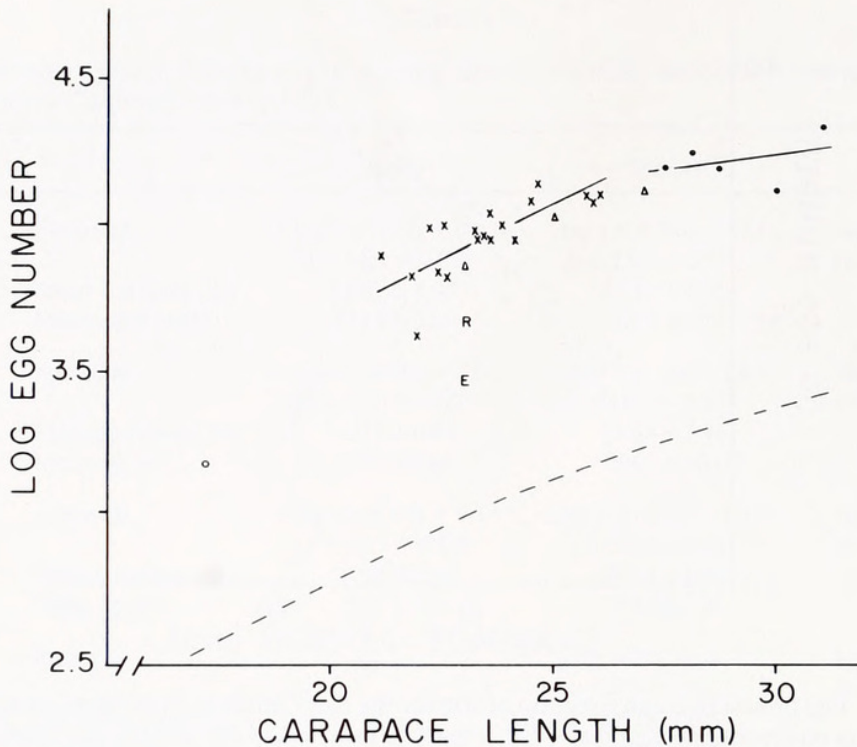


FIGURE 4. Egg production as a function of size for Pismo Beach crabs on 13 September 1982. Most symbols and broken line are as for Figures 2 and 3. The three triangles represent three data points from Eickstaedt (1969); the *R* and *E* symbols represent data points for Renata and El Tabo, Chile, South America (Osorio *et al.*, 1967).

October sample (Student's *t*-test; $P < 0.005$). By contrast, the mean number of eggs produced within each year class at Pismo (Table I, Student's *t*-test; $P < 0.005$) increased between the two sampling dates (17 May and 13 September), also while mean size of crabs increased. The time between samples was sufficiently long for full brood development in both cases; those data thus represent separate times of egg extrusion for each population sample. (Incubation time is less than 40 days; *e.g.*, Eickstaedt, 1969.)

No egg mass parasites were found in any of the samples.

Comparison of results with those obtained by other workers

Figures 2, 3, and 4 also contain a smooth broken line, derived from a straight line plot published by Efford (1969; Fig. 6). (His data were obtained from samples taken at various times during the reproductive season and from 20 different localities between Baja California, Mexico, and British Columbia, Canada.) In his figure, Efford had fitted a straight line on a log-log plot with unequal scaling for the two axes. After re-plotting on either standard log-log or on semi-logarithmic axes, the line becomes curved. The comparison shown here (Figs. 2–4) indicates that Efford's egg number estimates were approximately one-tenth the values obtained in the present study (Figs. 2–4).

As an additional comparison, egg count estimates are included in Figure 4 from Eickstaedt (1969) for 3 crabs of 23, 25, and 27 mm carapace length collected on 25 June 1968 in the Monterey area. Those values obtained by Eickstaedt correspond with the values we obtained for similar-sized second and third year crabs at Pismo Beach during 1982. Because his values differed so much from values obtained by

Efford for the same size crabs collected from that same area, Eickstaedt counted, rather than estimated, egg number in other clutches from 4 crabs of equivalent sizes collected in the same area on 10 June 1969 and obtained results similar to his earlier estimates.

Egg count results published by Osorio *et al.* (1967) for South American populations of *Emerita analoga* are also included in Figure 4; those counts were approximately 4–5 times greater than reported by Efford for similar-sized crabs. The mean number of eggs for El Tabo and Renaca crabs were significantly lower than our estimates in 9 comparisons out of 12 when compared to egg numbers for Goleta crabs (Student's *t*-test, $P < 0.05$). The animals within given year classes were larger at El Tabo and Renaca than those at Goleta, but they produced fewer eggs.

DISCUSSION

While many papers on crustacean biology have included data on the number of eggs produced as a function of size (*e.g.*, see Introduction), few have addressed the question of just how much variation can exist as a consequence of their indeterminate growth and multiple broods through time. One of the notable exceptions is the classic study of Paris and Pitelka (1962) on terrestrial isopods (*Armadillidium vulgare*). They found that the number of eggs produced by those isopods varied as a function of size/age class, season, and locality.

Marine crustaceans generally present a more formidable problem for egg production studies than terrestrial isopods, since year classes may be difficult to ascertain. Hippid crabs may be an exception. They have served as material for studies of population structure and egg production in the marine habitat (*e.g.*, Osorio *et al.*, 1967; Barnes and Wenner, 1968; Cox and Dudley, 1968; Efford, 1969; Eickstaedt, 1969; Subramoniam, 1977; Diaz, 1980; and Perry, 1980), but only to a limited extent.

Several features of hippid crab biology render them suitable for more full-scale investigations of population structure and egg production. They are hardy, often occur in great numbers (*e.g.*, Efford, 1976), can be collected easily, can be measured readily (Wenner *et al.*, 1974), and survive well in quality seawater systems. They live at least three years (3 years maximum for *Emerita analoga*; Siegel and Wenner, 1985), permitting separation of population structure into modal size classes (*e.g.*, Wenner and Fusaro, 1979), which appear to be year classes (Siegel and Wenner, 1985).

This study of egg production in *Emerita analoga* revealed that the relationship between egg number and length or width can be analyzed in conjunction with prior separation of the size frequency distribution into modal size/age classes. The modal year class separation permitted a more detailed analysis of egg production as a function of size than has prevailed before (*e.g.*, Efford, 1969; Eickstaedt, 1969). Additional information was provided by the modal separation approach, opening the way for quantitative comparisons of variation within season, between years, and between localities.

After data on egg number as a function of size had been plotted in all conventional manners, it was apparent that a power function was present and that the semi-log plot was an appropriate representation. That is because the linear measurement of either length or width, as is common in crustacean studies, is being compared to the number of eggs in a three-dimensional egg mass. In addition, a semi-logarithmic plot is more convenient for retrieving data than either the log-log plot or any plot involving the cube of the animal's length or width.

For the one population which had a full complement of three year classes of ovig-

erous crabs (Goleta), the slope of the regression line decreased with the size/age class of the animals. Without the modal size class breakdown, one could conclude that the relationship between egg production and size was curvilinear on a semi-log plot. However, the technique of splitting modes and analyzing egg production within each mode, as illustrated here, permits a biologically meaningful comparison of egg production by year classes between seasons, years, and localities.

Third year crabs were scarce at the San Clemente site, and the variation in the number of eggs produced by those few crabs was great. Both Auyong (1981) and Wenner (1982) reported a marked scarcity of third and sometimes even second year crabs in that area, especially at sites further south which were closer to the San Onofre Nuclear Generating Station. Those results suggested a failure at overwintering, which could be related to the disruption of egg production (Siegel and Wenner, 1984) in that area.

The modal separation approach can permit a resolution of apparent discrepancies in egg production results found for different localities and in different seasons. First year crabs apparently produce a single clutch of eggs at sites in the Southern California Bight before the end of summer (*e.g.*, Cox and Dudley, 1968; Siegel and Wenner, 1985). However, the time at onset of egg production of first year crabs may vary widely (see Cox and Dudley, 1968; Wenner *et al.*, 1985).

Crabs from Pismo Beach in Central California do not usually produce eggs until their second year on the beach (Fig. 4 and unpub. data), which may explain their larger size at sexual maturity in that region (Wenner *et al.*, 1985). The larger size at the onset of sexual maturity at Pismo Beach may be related both to a slower rate of ovarian development in cooler waters and to a faster growth rate brought about by greater food availability. Annala *et al.* (1980) also reported an inverse relationship between temperature and size at maturity in spiny lobsters (*Jasus edwardsii*) in New Zealand waters.

Second and third year crabs at Pismo Beach were larger and produced more eggs than their counterparts at Goleta and San Clemente. Other investigators have found such variation in crustacean egg production at different locations for similar-sized animals without separating population structure into constituent modal year classes (*e.g.*, Barnes and Barnes, 1968; Steele and Steele, 1975; Hill, 1977; Jones and Simons, 1983). Osorio *et al.* (1967) also found different egg numbers for sand crabs (*Emerita analoga*) of equivalent year classes at two sites in South America.

The seasonal differences found in egg numbers at Goleta and Pismo Beach were striking and similar to those found by Eickstaedt (1969) in a more limited study. Paris and Pitelka (1962) also reported such differences during the season in their study of isopod egg production. If such seasonal differences are common in animals which produce multiple broods during each reproductive season, calculation of life tables becomes a far more difficult matter than the traditional textbook examples would indicate.

Efford (1969) and Eickstaedt (1969) reported widely different values for the number of eggs produced by equivalent-sized crabs. Eickstaedt's concern about that discrepancy and subsequent direct counts (rather than estimates) indicated that Efford had erred. A replotting of Efford's regression line on the displays obtained in this study reveal that the values reported by Efford were approximately one order of magnitude lower than those obtained either by Eickstaedt or in this study. Eickstaedt (1969; pp. 86, 87) attributed the difference in estimated numbers to Efford's apparent failure to check his estimated values by direct counts.

An accurate estimate of the number of eggs produced by females in populations can be used to assess the effects of different environmental conditions within or be-

tween habitats (*e.g.*, Wenner and Fusaro, 1979). That measure includes the number of eggs produced per given size or age of animal and the total number of eggs produced per year by a representative population sample (*e.g.*, the number of eggs per representative thousand females). For animals with indeterminate growth, especially for crustaceans which possess no indication of age and which may produce multiple broods within a season, the task of estimating the number of eggs for a representative population sample and/or the reproductive output of a population requires a detailed analysis.

The results of this study indicate that a separation of size frequency distributions into constituent year classes can be done before one examines egg production as a function of size. This modal separation technique provides more information than the traditional method of analyzing egg production as a function of size without regard for age. Application of the technique can enhance seasonal, geographical, and environmental comparisons of variation in egg production, as well as aid in estimating total reproductive output.

ACKNOWLEDGMENTS

We thank M. Page and P. Wells for help on the manuscript and H. Caswell, A. Stewart-Oaten, and H. Wells for assistance on the statistical analysis. We also thank J. Stowe of the California Department of Parks and Recreation for permitting access to the sample site on park land (San Clemente State Beach) and D. Mustard for typing assistance.

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