**Abstract.**—Fecundity of the yellow rock crab *Cancer anthonyi* was examined seasonally over two years. Ovigerous crabs varied in size from 89 to 153 mm carapace width. Crabs held in the laboratory brooded more than three clutches per year without molting or mating. Crab fecundity varied seasonally, with peaks in late spring–early summer and late fall–early winter. Ovigerous crabs carried an estimated 0.73–3.30 million eggs, depending on crab size, stage of egg development, and season. The log body size–log fecundity relationship changed significantly with crab embryogenesis. Estimates of reproductive potential, defined in terms of the total number of eggs produced throughout the entire adult life span, were based on the mean number of eggs produced at the mean adult size, the minimum and maximum number of mature instars, the minimum and maximum number of broods per instar, and the number of broods oviposited per year. For a female *C. anthonyi*, it was 14.7–29.4 million eggs, which was relatively higher than other members of the genus.

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# Fecundity and the Reproductive Potential of the Yellow Rock Crab *Cancer anthonyi*

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The yellow rock crab *Cancer anthonyi* Rathbun, 1897, supports a growing fishery in southern California. The rock crab fishery exceeds 600 tons annually ($2 million ex-vessel value), with the Santa Barbara district representing 40–60% of the total catch (Resource Agency of California 1981–87, Carroll and Winn 1988). Three species of rock crabs comprise the fishery (*C. antennarius*, *C. anthonyi*, and *C. productus*), with *Cancer anthonyi* being most prevalent in catches in southern California (Winn 1985, Carroll and Winn 1988). At present, rock crabs are exploited with no restrictions on sex or reproductive condition; ovigerous and nonovigerous females are both removed by the fishery.

Little is known about the reproductive biology of most *Cancer* species (for review, see Shields 1991). We investigated fecundity and aspects of the reproductive biology of *Cancer anthonyi* as part of a larger study that examined brood mortality resulting from nemertean predation (Shields et al. 1990). We report observations on multiple broods per crab and interbrood periods, and present an analysis of crab fecundity in relation to size, embryogenesis, and seasonality. Lastly, we define reproductive potential in terms of the maximum lifetime fecundity of an individual crab, and compare reproductive potential within the genus.

## Methods

Ovigerous female crabs were trapped by a commercial fisherman at depths of 10–100 m from the Santa Barbara Channel, between Summerland and Gaviota, California (approximately 34°23′–34°25′N, 119°34′–120°12′W). Twenty to twenty-five female crabs were obtained at monthly or bimonthly intervals for two years (November 1981–November 1983). We sampled 345 ovigerous *Cancer anthonyi* of which 311 were completely processed (see Shields et al. 1990). Carapace width (CW) was measured, and the entire second left pleopod was excised and stored in 5% formalin in seawater for further analyses. Crabs were then released or maintained in flowing seawater aquaria for additional observations.

Embryogenesis was examined by observing embryos throughout the developmental process. The time to eclosion, interbrood period, and the effect of temperature on embryogenesis were examined in crabs maintained in aquaria with running seawater at normal oceanic temperatures. Crabs maintained in aquaria were fed market squid or mackerel weekly or biweekly. For statistical analyses, broods were grouped on the basis of the embryogenic development of attached eggs; i.e., embryos were in early (I–II), middle (III–IV), or late (V–VII) stages of development, or near hatching (VIII). Roman numerals refer to the developmental stages of embryogenesis (EDS) of Shields and Kuris (1988a) and Shields et al. (1990).

The term fecundity is here defined as the total number of live eggs carried by each female at any given time during incubation. Fecundity per pleopod was estimated as in Shields et al. (1990); it represents the number of live eggs on the 2d left pleopod. In addition, the actual fecundity per crab was determined for 12 crabs (96 pleopods). The fecundities of other crabs were then estimated using the regression of fecundity/pleopod with the fecundity of the 12 crabs.

Statistical analyses (ANOVA, ANCOVA, linear regression, Sidak's inequality) were conducted with the aid of SAS (1982). The log-transformation was used to reduce differences in variance between groups. A value of $P<0.05$ was accepted as significant. Data from all of the 2d left pleopods were statistically independent. Two statistics were used to minimize the influence of outliers on the analysis of covariance of log fecundity and log size between seasons, and between EDS groups. An outlier was removed from the ANCOVA and the subsequent regression analyses only if the value of its studentized residual was ± 1.50, the value of its Cooke's D influence statistic was greater than 0.006 (SAS 1982), and only if these statistics were consistent between transformed and untransformed data (5 outliers in early and middle embryogenesis). We suggest that the 5 outliers were bearing a second or third brood between molting and mating events, hence their fecundity was low (see below).

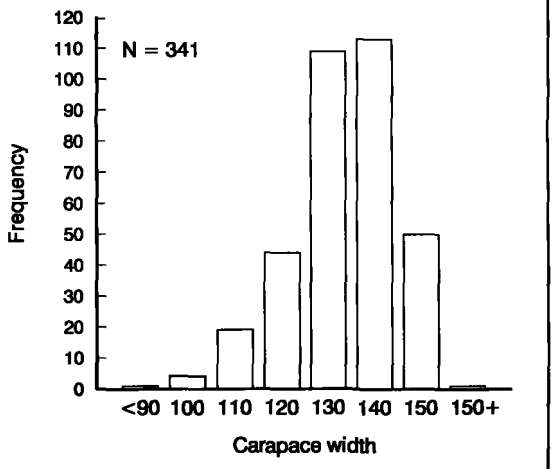


**Figure 1**
Size-frequency histogram of ovigerous *Cancer anthonyi* by 10-mm increments.

**Table 1**
Brood and interbrood period (days) for three groups of *Cancer anthonyi* females. Crabs were trapped while ovigerous, and the initial interbrood period was recorded after eclosion. All values are expressed as means (± SD); *N* = number of crabs. Numbers of crabs decreased within each group as a result of mortality.

| Group | Brood | Days | Temp. (°C) | *N* | Interbrood | Days | Temp. (°C) | *N* |
|---|---|---|---|---|---|---|---|---|
| A | | | | | | | | |
| | I | 40.7 ± 3.1 | 14.6 ± 1.1 | 16 | I | 42.9 ± 20.5 | 14.3 ± 0.7 | 16 |
| | II | 33.7 ± 4.1 | 16.6 ± 1.5 | 11 | II | 49.4 ± 18.1 | 15.3 ± 1.2 | 12 |
| B | | | | | | | | |
| | I | 51.8 ± 4.4 | 10.9 ± 1.9 | 13 | I | 45.9 ± 28.4 | 10.5 ± 1.3 | 15 |
| | II | 38.2 ± 3.5 | 13.1 ± 1.0 | 12 | II | 25.1 ± 5.2 | 12.6 ± 1.5 | 10 |
| | III | 45.6 ± 5.8 | 12.4 ± 0.9 | 9 | III | 48.0 ± 27.5 | 12.5 ± 0.7 | 10 |
| C | | | | | | | | |
| | I | 35.8 ± 3.8 | 14.9 ± 1.8 | 8 | I | 26.9 ± 9.6 | 14.1 ± 0.7 | 8 |
| | II | 34.3 ± 3.1 | 16.2 ± 1.6 | 3 | II | 55.0 ± 30.5 | 15.1 ± 1.6 | 7 |
| Total | | 40.0 ± 6.6 | 14.1 ± 2.1 | | | 41.9 ± 11.5 | 13.5 ± 1.6 | |
| | Range (29–58) | | | | Range (16–123) | | | |

## Results

### General observations

Ovigerous females varied from 89 to 153 mm in carapace width (Fig. 1), with a mode at 140 mm. Broods of *C. anthonyi* were oviposited without observed prior mating or molting by the female crab, and were observed for every mature crab held in the laboratory; some crabs brooded at least three clutches per year in the laboratory (Table 1). At a mean seawater temperature of 15°C, crab eggs took approximately 40 days to develop from oviposition to eclosion (Table 1). Subsequent broods were typically produced within 1–2 months after eclosion of the previous brood. Crab embryos from subsequent broods (second and third) were viable and hatched normally. In addition, the seminal receptacles of 24 crabs that were dissected after the eclosion of at least a second brood contained viable spermatozoa.

Broods oviposited in sand- and gravel-bottomed aquaria were smaller than those from crabs in the field (mean fecundity/pleopod = $2.75 \pm 0.73$(SD) $\times 10^5$, versus $4.10 \pm 0.67$ (SD) $\times 10^5$; $N = 12$ and 12, respectively; $t = 4.72$, $P < 0.001$); but food or holding effects may have confounded ovarian development and fecundity in lab-held crabs.

*Cancer anthonyi* brooded an estimated 0.73–3.30 million eggs per clutch depending on crab size. Crab fecundity (log fecundity/pleopod) was significantly different between broods in different stages of embryogenesis (Table 2; ANOVA, Sidak's inequality, $P < 0.05$). Clutch size did not differ significantly between broods in early and middle stages of development, hence these broods were combined for the size-fecundity analyses.

At eclosion, female crabs actively aided the hatching process. Females stood upon all of their legs and vigorously aerated their brood by agitating their abdomens and pleopods. Water currents through the gill chamber appeared to reverse their usual direction and flowed anteriorly through the egg mass. This facilitated eclosion, and pushed hatched prezoeae out of and away from the clutch. Within 2–3 days after hatching, female crabs stripped their pleopods of empty and dead eggs. The setae of cleaned pleopods attained a golden sheen comparable to their appearance on a freshly molted crab.

**Table 2**

Changes in log fecundity/pleopod with embryogenesis. EDS refers to developmental stages of embryogenesis [class 1, EDS I–II; class 2, EDS III–IV; class 3, EDS V–VII; class 4, EDS VIII] (Shields and Kuris 1988a, Shields et al. 1990). Days of development are based on temperatures of 15°C. Values with different letters are significantly different (ANOVA, Sidak's inequality, $P < 0.05$).

| EDS class | Days of development | $N$ | Fecundity/pleopod (log no. of eggs) ± SD | |
|---|---|---|---|---|
| 1 | 1–12 | 97 | 5.504 ± 0.200 | A |
| 2 | 13–30 | 129 | 5.517 ± 0.201 | A |
| 3 | 31–38 | 78 | 5.399 ± 0.239 | B |
| 4 | 39–40 | 31 | 4.748 ± 0.421 | C |

### Size-fecundity relationship

The fecundity per pleopod (log) was positively correlated with crab size (log CW) ($R$ 0.521, $P < 0.001$, $N$ 219; Fig. 2), but fecundity per crab (log) was not

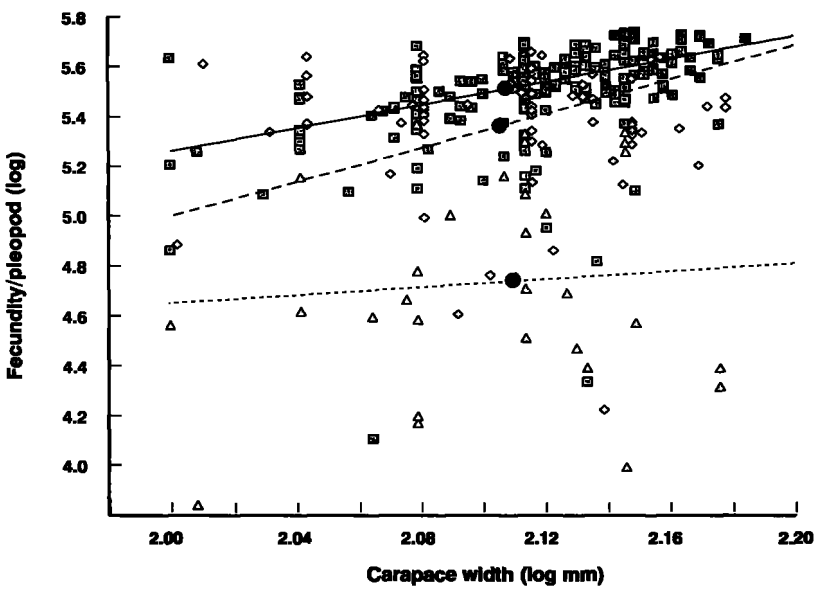


**Figure 2**

Size (CW)-fecundity relationships for *Cancer anthonyi* with broods in different stages of embryogenesis. Fecundities of crabs with eggs in early and middle stages of embryogenesis (boxes, solid line) and late embryogenesis (diamonds, dashed line) were highly correlated with crab size (in early and middle EDS, log fecundity/pleopod = 2.135(log CW) + 1.015, $R = 0.521$, $N = 219$; in late EDS, log fecundity/pleopod = 3.321(log CW) + 1.637, $R = 0.544$, $N = 70$; $P < 0.001$ for both). Fecundities of crabs with eggs near hatching (triangles, dotted line) were not correlated with size (log fecundity/pleopod = 0.723(log CW) + 3.217, $R = 0.055$, $N = 30$, $P > 0.05$). See text for ANCOVA results.

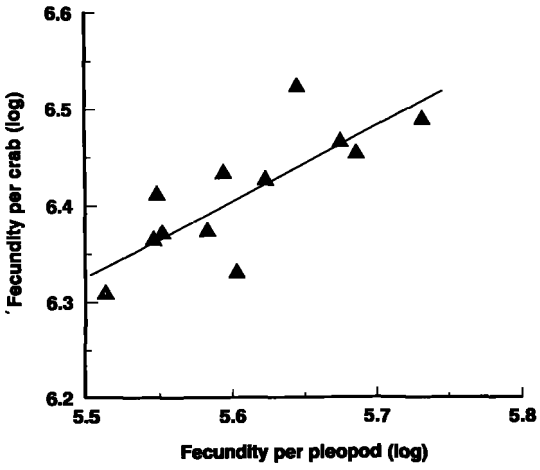


**Figure 3**

Relationship between fecundity per pleopod (X) and fecundity per crab (Y) for 12 crabs (log Y = 2.124 + 0.765 log X, $R$ = 0.782, $N$ = 12, $P<0.01$). The regression equation was used to calculate fecundity per crab for estimates of reproductive potential for *Cancer anthonyi*.

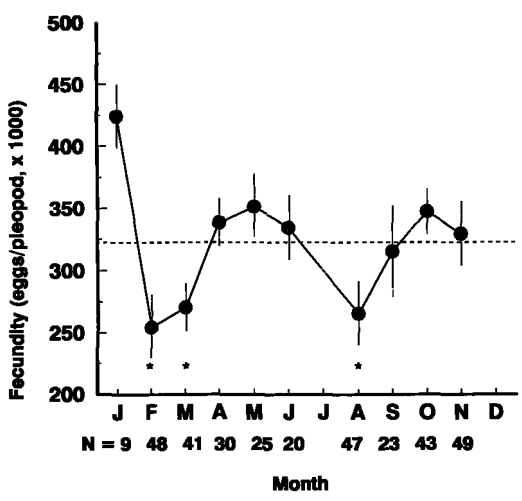


**Figure 4**

Seasonal variation in the fecundity per pleopod of *Cancer anthonyi*. Months with significantly less fecundity than other months are denoted with an asterisk (ANOVA, Sidak's inequality, $P<0.05$). Bars represent standard error of the mean; $N$ = sample size; dashed line = mean fecundity.

correlated with crab size ($R$ 0.449, $P>0.05$, $N$ 12). The partial correlation of fecundity with crab size was significant when fecundity per pleopod was held constant (partial correlation: $R$ 0.635, $P<0.05$, $N$ 12). Thus, projections of reproductive potential (based on estimates of the fecundity per crab) were derived from the correlation of fecundity per pleopod with fecundity (Fig. 3).

In addition, the relationship between fecundity per pleopod and crab size was significantly influenced by embryogenesis (Fig. 2). Slopes of the regressions and adjusted mean fecundities were significantly different between EDS groups (ANCOVA, adjusted means, $F_{(2,315)} = 224.57$, $P<0.01$; separate slopes, $F = 62.71$, $P<0.01$). Fecundity was not correlated with crab size when hatching was imminent (Fig. 2).

### Seasonal relationships

Crab fecundity varied seasonally (Fig. 4). Fecundity data from both years were combined for the seasonal analysis since their seasonal patterns were similar (ANOVA, log transformation, between years, within months, $P>0.05$). In February, March, and August, the mean fecundity/pleopod was lower than at other times of the year (ANOVA, log transformation, Sidak's inequality by month, $P<0.01$). The differences in mean fecundity/pleopod cannot be attributed to differences in crab size (CW) or developmental stage (EDS) during those months (two-way ANOVA with interaction, $P>0.05$, n.s.); they represent seasonal fluctuation in crab fecundity.

The size-fecundity relationship was significantly affected by seasonality. Crabs in late-winter and late-summer months (February, March, and August) brooded significantly fewer eggs than crabs of similar size in other months (ANCOVA, adjusted means of log fecundity/pleopod = 5.522 ± 0.012 (SE) versus 5.564 ± 0.006, respectively, $P<0.0025$). The slopes of the regression of log size on log fecundity/pleopod were also different between seasons (ANCOVA, separate slopes analysis, $b_{winter-summer}$ = 1.556 versus $b_{spring-fall}$ = 2.573, $P<0.001$). While these data show significant statistical variations, their biological significance remains speculative.

## Discussion

Most *Cancer* crabs carry a single brood through a single reproductive season. While multiple ovipositions after a single mating have been reported, they generally occur in two or more reproductive seasons (Williamson 1904, Knudsen 1964, Krouse 1972, Haefner 1976, Ebert et al. 1983). Indeed, multiple ovipositions during a single reproductive season have only been reported for *C. anthonyi* (this study), *C. antennarius*

(Shields, Okazaki, and Kuris, pers. observ.), and *C. productus* (Knudsen 1964).

Ovigerous *Cancer anthonyi* occur throughout the year in southern California. The proportion of ovigerous females in the female crab population varied seasonally, with a peak in the number of ovigerous crabs in March and a nadir in the ovigerous population in June (Reilly 1987). Crab fecundity, however, followed an opposite pattern. *Cancer antennarius*, which has a geographic range similar to *C. anthonyi*, bears eggs throughout the year with a peak in reproduction during the winter months (Carroll 1982).

Ovigerous *C. anthonyi* were highly fecund. Although body size and fecundity are highly correlated in the Brachyura (Hines 1982), for *Cancer* the larger crabs *C. magister* and *C. pagurus* bear relatively fewer eggs than *C. anthonyi* (Table 4). Differences in fecundity may be partially explained by differences in egg and zoea I size, and the duration of embryogenesis (Table 3), which in turn may be explained by climatic regime (Hines 1986). While the data remain incomplete, we note two general patterns: (1) Some species of *Cancer* produce many small eggs (higher fecundity) that quickly develop into small larvae, and (2) some species produce relatively larger eggs (lower fecundity) that slowly develop into large larvae.

Decreases in fecundity per pleopod during embryogenesis are mostly a result of nemertean predation or mechanical abrasion (Shields et al. 1990). The decrease is apparently related to crab size; larger crabs appear to lose relatively fewer eggs throughout embryogenesis than do smaller crabs. The impact of nemertean predators on the fecundity of the shore crab *Hemigrapsus oregonensis*, was also greater on smaller crabs (Shields and Kuris 1988b). While smaller crabs may be more numerous in a population (e.g., Gutierrez and Zuniga

**Table 3**

Comparative features of embryogenesis (diapause, D), egg size (widest diameter), length of zoea I, duration of larval development (zoea I to megalopae), female size at maturity, and fecundity for ten species of *Cancer*. Unknown data are indicated (?).

| Species | Embryogenic development (in days) | Egg diameter (μm) | Zoea I length* (mm) | Larval development (in days) |
|---|---|---|---|---|
| *C. antennarius*[1] | 50–60 | ? | 1.3 | ? |
| *C. anthonyi*[2] | 29–58 | 265–300 | 1.2 | 33–45 |
| *C. borealis*[3] | ? | 305 | 1.2 | ? |
| *C. gracilis*[4] | ? | ? | 1.2 | ? |
| *C. irroratus*[5] | 176–235 (*D*) | ? | 1.5 | ? |
| *C. magister*[6] | 90–120 | 400–440 | 2.5 | 45–160 |
| *C. oregonensis*[7] | 103–118 | ? | ? | ? |
| *C pagurus*[8] | 235–265 (*D*) | 450–500 | 1.8 | 35+** |
| *C productus*[9] | ~120 | ? | 1.8 | ~95 |
| *C. setosus*[10] | ? | 450 | ? | ? |

*Length of zoea I is carapace vertex to telson tips. Data from Ingle (1981).
**Does not include duration of megalopa stage.

References: [1]Carroll 1982, Shields et al. unpubl. data; [2]This study, Anderson and Ford 1976; [3]Haefner 1977, Carpenter 1978; [4,7,9]Knudsen 1964; [4,6,7,9]Orensanz and Gallucci 1988; [5]Shotton, 1973, Krouse 1976, Haefner 1976, Reilly and Saila 1978, Campbell and Eagle 1983; [6]Wild 1983abc, Hankin et al. 1985, Shirley et al. 1988; [8]Edwards 1979, Brown and Bennett 1980, Nichols et al. 1982, Le Foll 1986; [9]Toole 1985; [10]Gutierrez and Zuniga 1976.

**Table 4**

Range in size of ovigerous females, number of broods per instar, maximum number of adult instars, estimated range in fecundity per brood, and individual reproductive potential in various *Cancer* crabs. Unknown data are indicated (—), incomplete data (?), and numbers in parentheses represent the potential number of broods in later instars. For key to references, see Table 3.

| Species | Size (mm CW) | Broods per instar | Max. avg. no. adult instars | Est. range in fecundity per brood | Individual reproductive potential (eggs) |
|---|---|---|---|---|---|
| *C. antennarius*[1] | 116–143 | 1–2 | 5 | $\sim 1.0 \times 10^6$ | $5.0–10.0 \times 10^6$ |
| *C anthonyi*[2] | 90–153 | 2–3 | 3–4 | $0.7–3.3 \times 10^6$ | $14.7–29.4 \times 10^6$ |
| *C. borealis*[3] | 105–135 | 1 (?) | — | $0.3–1.6 \times 10^6$ | — |
| *C gracilis*[4] | 54–100 | 1 (2) | 2 | ? | — |
| *C. irroratus*[5] | 21–100 | 1 | 1–6? | $4.4–567.7 \times 10^3$ | $1.7–2.1 \times 10^6$ |
| *C. magister*[6] | 110–170 | 1 (2) | 3–4 | $0.5–1.5 \times 10^6$ | $3.0–4.0 \times 10^6$ |
| *C. oregonensis*[7] | 10–43 | 1 (2) | 6 | $1.0–3.3 \times 10^4$ | $<0.2 \times 10^6$ |
| *C. pagurus*[8] | 133–205 | 1 (3) | 3? | $0.5–3.0 \times 10^6$ | $5.3–8.7 \times 10^6$ |
| *C. productus*[9] | 70–129 | 1 (2) | 3 | ? | — |
| *C. setosus*[10] | 83–151 | 1 (?) | 2–3? | $0.6–1.7 \times 10^6$ | $2.3–3.5 \times 10^6$ |

1976, Hankin et al. 1985), their overall contribution to the production of planktonic larvae may be relatively equal to or less than that of the less-abundant larger females whose eggs may have a greater chance of surviving embryogenesis.

*Cancer anthonyi* has a high reproductive potential (Table 4). Estimates of reproductive potential are typically based on the growth, size at maturity, longevity, and fecundity of an animal (Campbell and Robinson 1983). These estimates have been applied to animals having but a single brood per year. Here, we define reproductive potential for an animal capable of producing more than one brood per year (reproductive potential: mean number of eggs produced at mean adult size, minimum and maximum number of mature instars, minimum and maximum number of broods per instar, and the estimated number of broods per year). We use the **maximum** or **entire** adult life span because (1) late instar females may contribute most to the overall egg production of their cohort, (2) estimates of adult mortality are unknown for most species, and (3) confounding correlations between fecundity and mortality are eliminated (Shields 1991). While admittedly crude, the estimates of reproductive potential are useful for comparisons (Table 4). The reproductive potential of a single female *C. anthonyi* was estimated at 14.7–29.4 million eggs in her lifetime (2.6 million eggs/brood at mean size, 3–4 broods/year, 2–4 reproductive years). *Cancer magister* has an estimated potential of approximately 3–5 million eggs (1–1.5 million eggs/brood, 1 brood/year, 3 reproductive years; MacKay 1942). Neither of these estimates consider smaller broods from older instars or variations in brood size within an instar.

Most *Cancer* crabs breed but once a year, making study of their reproduction and reproductive habits logistically difficult. The high fecundity and great reproductive potential of *Cancer anthonyi*, coupled with its frequent production of eggs, may provide an excellent model for the study of reproduction in *Cancer* crabs.

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