

## FECUNDITY AND REPRODUCTIVE OUTPUT IN TWO SPECIES OF DEEP-SEA CRABS, *GERYON FENNERI* AND *G. QUINQUEDENS* (DECAPODA: BRACHYURA)

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### ABSTRACT

Brood weight, fecundity, and egg size as a function of female body size were compared in the deep-sea red crab *Geryon quinquedens* and the deep-sea golden crab *Geryon fenneri*. Females of *G. fenneri* attained a larger body size than *G. quinquedens*, and body size in both species was the main determinant of reproductive output (brood mass) and fecundity per brood. Both species differed from most other brachyurans in having larger reproductive outputs, larger eggs, and lower fecundities relative to their large body sizes. After statistical adjustment for differences in body size between the two species, *G. quinquedens* had space in the body cavity for yolk accumulation and a brood mass which were 50% larger than *G. fenneri*. *Geryon quinquedens*, however, produced eggs 2.18 times the volume of *G. fenneri*, resulting in equivalent number of eggs per brood in similar-sized crabs. Large, yolky eggs in *G. quinquedens* are likely to contribute to the nutritional flexibility of its larvae, but apparently have coevolved with significant changes in female morphology and reproductive output.

Body size of female brachyuran crabs is the principal determinant of fecundity per brood and reproductive output (brood mass), with brood weight apparently being constrained to about 10% of female body weight by the space available for yolk accumulation in the cephalothorax (Hines, 1982). Egg size is the major reproductive variable which determines whether the relatively constrained brood mass is partitioned into many small or few large eggs, thus resulting in much greater variation in fecundity than in brood mass for equivalent-sized crabs (Hines, 1982). Ecological and evolutionary consequences of these apparent covariations have not been examined for closely related species in similar habitats (Hines, 1986a).

Deep-sea species of invertebrates generally have larger, more yolky eggs with either lecithotrophic or direct development than shallow-water counterparts in which planktotrophic development prevails (Thorson, 1950; Mileikovskiy, 1971; Hines, 1986b). Deep-water crustaceans similarly tend to have larger eggs than shallow-water species (Corey, 1981; Mauchline, 1973; Hines, 1986a; Van Dover and Williams, in press). Despite over 35 years of interest in reproductive and life-history patterns of deep-sea invertebrates, relatively few data are available on the reproductive biology of deep-water brachyurans.

This study compares brood weight, fe-

cundity per brood, and egg size as a function of female body size of the deep-sea red crab *Geryon quinquedens* and the deep-sea golden crab *G. fenneri*. These two species occur along the east and Gulf of Mexico coasts of North America on the outer continental shelf and slope at depths of 200 to >1,000 m (Haefner, 1978; Gerrior, 1981; Soto, 1985; Wenner *et al.*, 1987; Lockhart, 1988). Both species support small commercial fisheries (Haefner, 1978; Otwell *et al.*, 1984). Off the southeast and Gulf coast of North America, *G. quinquedens* occurs deeper than *G. fenneri*, with little overlap in the depth distribution of the two species (Soto, 1985; Lockhart, 1988; personal communications from W. Lindberg, University of Florida, Gainesville, and E. Wenner, Marine Resources Research Institute, Charleston, South Carolina). Both species have a peak season of brooding in fall through winter, with *G. fenneri* producing a single brood per year and *G. quinquedens* additionally having low levels of brooding year-round (Haefner, 1978; Wenner *et al.*, 1987; Hirsch, 1988; Erdman and Blake, 1988). Eggs of *G. quinquedens* are the largest known among marine brachyuran species with planktonic development (Hines, 1982, 1986a).

### MATERIALS AND METHODS

A sample of 17 ovigerous *Geryon quinquedens* was collected in traps in November 1979 off Massachusetts at a depth of 620 m. A similar sample of 12 ovigerous

Table 1. Summary of size and reproductive regressions for two species of *Geryon*.

	<i>Geryon fenneri</i>	<i>Geryon quinquedens</i>
Female size		
$\bar{x}$ (range) carapace width	124 (110–143)	106 (90–118)
Dry body wt = b(carapace width) + c	$Y = 0.0059X + 1.29$	$Y = 0.0089X + 0.877$
$r^2$	0.94	0.46
Body cavity volume		
Log body vol = b(log body wt) + c	$Y = 1.229X - 0.602$	$Y = 1.058X - 0.100$
Egg size		
$\bar{x}$ ( $\pm$ SD) diameter ( $\mu$ m)	567 ( $\pm$ 15)	731 ( $\pm$ 28)
Dry brood weight (g)		
Log brood wt = b(log body wt) + c	$Y = 1.453X - 1.680$	$Y = 0.997X - 0.636$
$r^2$	0.77	0.69
Fecundity per brood		
Log no. eggs = b(log body wt) + c	$Y = 1.279 + 2.927$	$Y = 0.901X + 3.558$
$r^2$	0.48	0.61

*G. fenneri* was collected in traps in September 1986 off the west coast of Florida at a depth of 366 m. The samples were frozen and then fixed in 10% Formalin-sea water and stored in 70% ethanol until they were processed. Brooded embryos of all sampled crabs of both species were selected in the same late blastula to early gastrula developmental stage in order to avoid confounding effects of embryonic diameters swelling during late stages of development. Processing followed the method of Hines (1982), in which the following variables were measured for each crab: dry body weight (g) of the female; maximum carapace width (mm) of the female; dry weight (g) of the brooded egg mass; average volume ( $\text{mm}^3$ ) of an egg, calculated for a sphere with the mean diameter including the chorionic membrane tightly adhering to the embryonic surface of a subsample of 7 eggs before drying; and the number of eggs per brood, extrapolated from the dry weights of the total brood and of a counted subsample of about 2,000 eggs. All samples were oven-dried to constant weight at 60°C. For a subset of the sample of each species, the volume of the body cavity was measured following the method of Hines (1982) in which the volume of soft modeling clay necessary to fill the space occupied by the viscera and gonads was measured. Data were analysed with regressions of log-log transformations for allometric plots ( $Y = cX^b$ ;  $\log Y = b \log X + c$ ) of reproductive variables versus dry body weight. Comparisons of different-sized crabs utilized ANCOVA with female body weight as the covariate as discussed in Hines (1982).

## RESULTS

Mean size of female *Geryon fenneri* was significantly larger than that of *G. quinquedens*, with a mean dry body weight of 93 g for the former and 68 g for the latter (Table 1, Fig. 1A; ANOVA:  $F_{(1,33)} = 28.24$ ,  $P < 0.001$ ). However, the size range of the two species overlapped substantially. Volume of the body (i.e., cephalothorax) cavity in-

creased significantly with body weight in both species (Fig. 2; ANOVA: *G. fenneri*,  $F_{(1,4)} = 38.58$ ,  $P < 0.01$ ; *G. quinquedens*,  $F_{(1,3)} = 88.65$ ,  $P < 0.01$ ); but slopes of the regressions did not differ significantly between species (ANCOVA:  $F_{(1,7)} = 0.91$ ,  $P > 0.3$ ). When volume of the body cavity was adjusted statistically for body weight, it was significantly larger in *G. quinquedens* than in *G. fenneri* by about 50%, with a least squares mean of 83.2  $\text{cm}^3$  in the former and 55.3  $\text{cm}^3$  in the latter (Table 1, Fig. 1B; ANCOVA:  $F_{(1,7)} = 6.03$ ,  $P < 0.05$ ).

Egg size varied little within individual broods of either species ( $SD < 4\%$  of  $\bar{x}$ ). Egg size did not differ significantly among individuals within a species (nested ANOVA:  $F_{(28,176)} = 1.01$ ,  $P > 0.3$ ); however, the egg volume of *Geryon quinquedens* at 0.205  $\text{mm}^3$  was 2.18 times larger than that of *G. fenneri* at 0.094  $\text{mm}^3$  (Table 1, Fig. 1C; ANOVA:  $F_{(1,29)} = 422.88$ ,  $P < 0.001$ ).

Brood weight increased significantly with female body weight for both species (Fig. 3, Table 1; ANOVA: *Geryon fenneri*,  $F_{(1,10)} = 34.07$ ,  $P < 0.001$ ; *G. quinquedens*,  $F_{(1,15)} = 32.42$ ,  $P < 0.001$ ); however, regression slopes did not differ significantly between species (ANCOVA:  $F_{(1,26)} = 2.16$ ,  $P > 0.1$ ). Brood weights for mean-sized females of each species were nearly equal at 14.9 g for *G. fenneri* and 15.2 g for *G. quinquedens* (Fig. 1D). When adjusted for differences in female body size, the least squares mean brood weight in *G. quinquedens* at 17.4 g was significantly larger by 53% than in *G.*

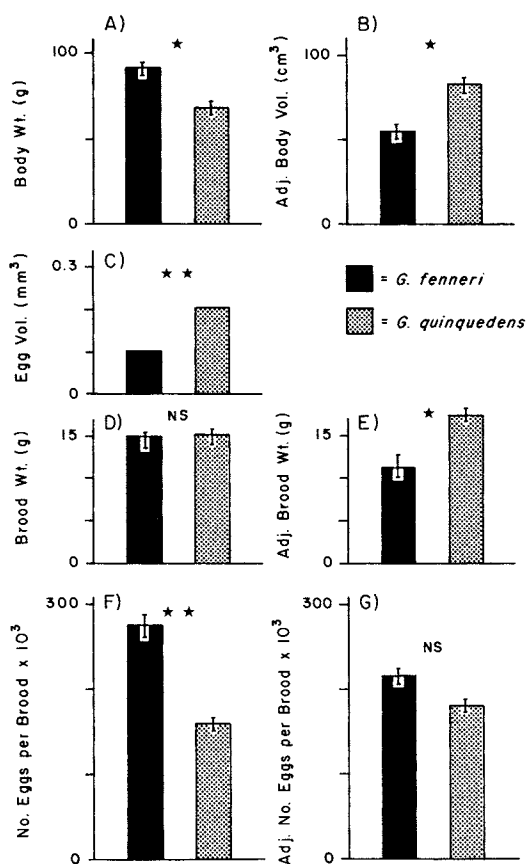


Fig. 1. Comparison of body size and reproductive variables for *Geryon fenneri* and *Geryon quinquedens*. A) Dry body weight. B) Volume of body cavity adjusted by ANCOVA for body size. C) Volume of an egg. D) Dry brood weight for an average-sized female. E) Dry brood weight adjusted by ANCOVA for body size. F) Fecundity per brood for an average-sized female. G) Fecundity per brood adjusted by ANCOVA for body size. Histograms show means or least squares means with standard error bars. Significance levels for differences between the means of the two species, as tested by ANOVA and ANCOVA, are indicated as: NS = not significant; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ .

*fenneri* at 11.4 g (Fig. 1E; ANCOVA:  $F_{(1,26)} = 5.88$ ,  $P < 0.05$ ). The average female *G. quinquedens* invested about 22% of her dry body weight in eggs per brood, while *G. fenneri* invested about 16%.

Fecundity per brood increased significantly with female body size in both species (Fig. 3, Table 1; ANOVA: *Geryon fenneri*,  $F_{(1,10)} = 9.37$ ,  $P = 0.01$ ; *G. quinquedens*,  $F_{(1,15)} = 23.46$ ,  $P < 0.001$ ); however, regression slopes did not differ significantly between species (ANCOVA:  $F_{(1,26)} = 0.85$ ,  $P$

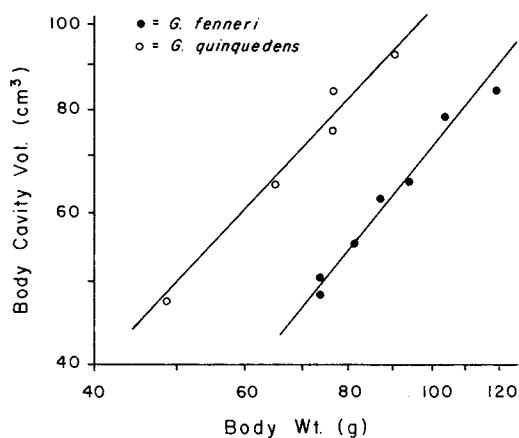


Fig. 2. Comparison of volume of body cavity as a function of body size for *Geryon fenneri* and *Geryon quinquedens*. Regression equations are given in Table 1. Solid symbols = *G. fenneri*; open symbols = *G. quinquedens*. Note log scales of axes.

$> 0.3$ ). Although *G. fenneri* had significantly greater numbers of eggs per female than *G. quinquedens*, the difference was attributable to the larger body sizes of *G. fenneri*. A mean-sized female *G. fenneri* produced about 73% more eggs at 275,700 per brood than a smaller mean-sized female *G. quinquedens* at 159,100 eggs per brood (Fig. 1F). When fecundity was adjusted for body size, the number of eggs per brood did not differ significantly between species, with least squares means of 216,800 eggs for *G. fenneri* and 179,600 eggs for *G. quinquedens* (Fig. 1G; ANCOVA:  $F_{(1,26)} = 0.64$ ,  $P > 0.4$ ).

#### DISCUSSION

As in other brachyurans (Hines, 1982), female body size was the principal determinant of reproductive output and fecundity in the sampled *Geryon fenneri* and *G. quinquedens*. Larger females produced larger brood masses and had greater fecundity per brood than smaller crabs, both within species and between species. Both species have large body size and produce hundreds of thousands of larvae per female per year, but females of *G. fenneri* grow larger than female *G. quinquedens* (Table 1, Fig. 1; Haefner, 1978; Manning and Holthius, 1984; Wenner *et al.*, 1987). The increase in brood weight and fecundity exhibited positive allometric relationships (i.e., increasing proportion with increasing body size) in

*G. fenneri* and approximately isometric relationships (i.e., equal proportion with increasing body size) in *G. quinquedens*, as indicated by the slopes of the regressions of log reproductive variable versus log body weight (Fig. 3; see also Hines, 1982).

These two species differ from most other brachyurans in several important variables. Their brood masses at 16% and 22% of body weight are considerably larger than the overall average of 10% (range 5–18%) for 21 species in my earlier study (Hines, 1982). They also had relatively large eggs at 560 and 730  $\mu\text{m}$  in diameter, but rather low fecundity at 160,000–275,000 eggs per brood for such large crabs. For example, comparably sized portunid or cancrid species typically produce 1,000,000–3,000,000 eggs which are 200–400  $\mu\text{m}$  in diameter (Hines, 1982; unpublished data).

Despite these differences from other brachyurans, the two species of *Geryon* exhibited a pattern of constraints and covariation among reproductive variables that is consistent with the pattern among other crabs (Hines, 1982). Brood size appears to be limited by space available within the cephalothorax for yolk accumulation, because the larger reproductive output of the two species of *Geryon* was correlated with a larger volume of the body cavity compared to the other species measured in my earlier study (Hines, 1982). For each species, the allometry of brood weight closely approximated the allometry of the volume of the body cavity, just as the overall allometry of brood mass approximated that of body cavity volume among species in the earlier study. In addition, the 50% larger brood mass of *G. quinquedens* was matched with a 50% larger volume of the body cavity compared to *G. fenneri*. Despite the significantly larger brood mass relative to body size in *G. quinquedens*, its very large egg size resulted in a size-specific fecundity which was not greater than *G. fenneri*. Conversely, as a result of having an egg with half the volume of that of *G. quinquedens*, *G. fenneri* had a size-specific fecundity equivalent to *G. quinquedens* while producing a brood mass only about half that of *G. quinquedens*.

The larval development of *Geryon fenneri* has not been studied, but larval development in *G. quinquedens* exhibits a high degree of "nutritional flexibility," the ability

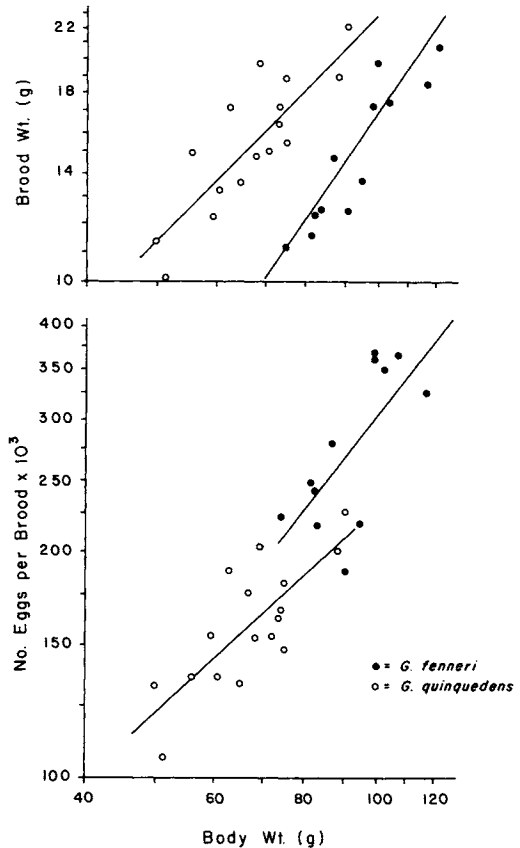


Fig. 3. Comparisons of dry brood weight (top) and fecundity per brood (bottom) as a function of body size for *Geryon fenneri* and *Geryon quinquedens*. Regression equations are given in Table 1. Solid symbols = *G. fenneri*; open symbols = *G. quinquedens*. Note log scales of axes.

to survive to metamorphosis on relatively low quality food (rotifers) (Sulkin and Van Heukelem, 1980). Differences in larval responses to nutritional fluctuations can have important adaptive significance for brachyuran development (Anger *et al.*, 1981). The large eggs of the two species of *Geryon* may be lecithotrophic adaptations which help to provide nutritional flexibility to larvae hatched in the deep sea. The very large egg in *G. quinquedens* could provide the nutritional flexibility which is presumably necessary for this species to exist in the deep sea of temperate and boreal waters of the northwest Atlantic. As a species distributed at low latitudes, larvae of *G. fenneri* may encounter more predictably abundant food resources in the overlying subtropical to

tropical waters, thus selecting for a smaller parental investment per egg.

Considerations of physical or "design" constraints (*sensu* Stearns, 1977) pertaining to allometric relationships are important in a wide variety of invertebrate reproductive patterns (Perron and Corpuz, 1982; Chaffee and Strathmann, 1984; Strathmann and Chaffee, 1984; Strathmann *et al.*, 1984; Kabat, 1985; Hines, 1986b). I hypothesize that adaptation of large eggs for nutritional flexibility in *Geryon quinquedens* exploiting the deep sea at high latitudes has led to evolutionary ramifications in the adult morphology and reproductive tactics of this species. In order for fecundity not to be reduced excessively by partitioning the brood into very large eggs, *G. quinquedens* apparently has evolved increased space in the cephalothorax to accumulate yolk for a significantly larger brood mass than most brachyurans. Although fecundity could also be increased by producing additional broods per year (Hines, 1982), species in the family Geryonidae appear to be limited to low levels of brood production per year by energetically restricted food resources in the deep sea (e.g., Thorson, 1950), by restrictive timing of larval release at the time of the spring plankton bloom (e.g., Barnes, 1957), and/or by phylogenetic constraints (e.g., Hines, 1986a). The timing of brooding in winter and larval release in spring by *G. fenneri* at low latitudes (Hinsch, 1988) and at least low levels of brooding year-round in *G. quinquedens* indicate, however, that reproductive patterns of deep-sea crabs are complex.

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#### LITERATURE CITED

- Anger, K., R. R. Dawirs, V. Anger, and J. D. Costlow. 1981. Effects of early starvation periods on zoeal development of brachyuran crabs.—*Biological Bulletin* 161: 199–212.
- Barnes, H. 1957. Processes of restoration and synchronization in marine ecology: the spring diatom increase and the spawning of the common barnacle, *Balanus balanoides*.—*Année Biologique* 33: 67–85.
- Chaffee, C., and R. R. Strathmann. 1984. Constraints on egg masses. I. Retarded development within thick egg masses.—*Journal of Experimental Marine Biology and Ecology* 84: 73–83.
- Corey, S. 1981. Comparative fecundity and reproductive strategies in seventeen species of the Cumacea (Crustacea: Peracarida).—*Marine Biology* 62: 65–72.
- Erdman, R., and N. J. Blake. 1988. Reproductive ecology of female golden crabs, *Geryon fenneri* Manning and Holthuis, from southeastern Florida.—*Journal of Crustacean Biology* 8: 392–400.
- Gerrior, P. 1981. The distribution and effects of fishing on the deep-sea red crab, *Geryon quinquedens* Smith, off southern New England.—M. Sc. thesis, Southeastern Massachusetts University, North Dartmouth, Massachusetts. Pp. 1–130.
- Haefner, P. A., Jr. 1978. Seasonal aspects of the biology, distribution, and relative abundance of the deep-sea red crab, *Geryon quinquedens* Smith, in the vicinity of the Norfolk Canyon, western North Atlantic.—*Proceedings of National Shellfisheries Association* 68: 49–62.
- Hines, A. H. 1982. Allometric constraints and variables of reproductive effort in brachyuran crabs.—*Marine Biology* 69: 309–320.
- . 1986a. Larval patterns in the life histories of brachyuran crabs (Crustacea, Decapoda, Brachyura).—*Bulletin of Marine Science* 39: 444–466.
- . 1986b. Larval problems and perspectives in life histories of marine invertebrates.—*Bulletin of Marine Science* 39: 506–525.
- Hinsch, G. W. 1988. Morphology of the reproductive tract and seasonality of reproduction in the golden crab *Geryon fenneri* from the eastern Gulf of Mexico.—*Journal of Crustacean Biology* 8: 254–261.
- Kabat, A. R. 1985. The allometry of brooding in *Transennella tantilla* (Gould) (Mollusca: Bivalvia).—*Journal of Experimental Marine Biology and Ecology* 91: 271–279.
- Lockhart, F. D. 1988. Depth, distribution, and ecology of *Geryon* spp. (Brachyura, Geryonidae) in the eastern Gulf of Mexico.—M.S. thesis, University of Florida, Gainesville, Florida. Pp. 1–52.
- Manning, R. B., and L. B. Holthuis. 1984. *Geryon fenneri*, a new deep-water crab from Florida (Crustacea: Decapoda: Geryonidae).—*Proceedings of the Biological Society of Washington* 97: 666–673.
- Mauchline, J. 1973. The broods of British Mysidacea (Crustacea).—*Journal of the Marine Biological Association of the United Kingdom* 53: 801–817.
- Mileikovsky, S. A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a reevaluation.—*Marine Biology* 10: 193–213.
- Otwell, W. S., J. Bellairs, and D. Sweat. 1984. Initial development of a deep-sea crab fishery in the Gulf of Mexico.—Florida Sea Grant College Report No. 61: 1–29.
- Perron, F. E., and G. C. Corpuz. 1982. Costs of parental care in the gastropod *Conus pennaceus*: age-specific changes and physical constraints.—*Oecologia* 55: 319–324.
- Soto, L. A. 1985. Distributional patterns of deep-

- water brachyuran crabs in the Straits of Florida.—*Journal of Crustacean Biology* 5: 480–499.
- Stearns, S. C. 1977. The evolution of life history traits.—*Annual Review of Ecology and Systematics* 8: 145–171.
- Strathmann, R. R., and C. Chaffee. 1984. Constraints on egg masses. II. Effect of spacing, size, and number of eggs on ventilation of masses of embryos in jelly, adherent groups, or thin-walled capsules.—*Journal of Experimental Marine Biology and Ecology* 84: 85–93.
- , M. F. Strathmann, and R. H. Emson. 1984. Does limited brood capacity link adult size, brooding, and simultaneous hermaphroditism? A test with the starfish *Asterina phylactica*.—*American Naturalist* 123: 796–818.
- Sulkin, S. D., and W. F. Van Heukelem. 1980. Ecological and evolutionary significance of nutritional flexibility in planktotrophic larvae of the deep sea red crab *Geryon quinquedens* and the stone crab *Menippe mercenaria*.—*Marine Ecology—Progress Series* 2: 91–95.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates.—*Biological Reviews* 25: 1–45.
- Van Dover, C. L., and A. B. Williams. (In press.) Egg size in squat lobsters (Galatheoidea): constraints and freedom.—*In*: A. M. Wenner and A. M. Kuris, eds., *Crustacean egg production*. Crustacean issues. Balkema Press, Rotterdam.
- Wenner, E. L., G. F. Ulrich, and J. B. Wise. 1987. Exploration for golden crab, *Geryon fenneri*, in the South Atlantic Bight: distribution, population structure, and gear assessment.—*Fishery Bulletin, United States* 85: 574–560.

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