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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^{1, 2}

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ABSTRACT

Deep-sea red crabs were collected from demersal trawl surveys of Norfolk Canyon and an adjacent open slope area in the Chesapeake Bight of the western North Atlantic Ocean. The surveys were made in each of four seasons over a period of three years. The 2539 red crabs caught ranged from 16mm to 143 mm in carapace length (CL). Relationships between CL and carapace width (CW) were derived for 308 males and for 269 females. Wet weight to CL relationships were derived for 238 males and for 142 females.

Red crabs were contagiously distributed within the total depth range of capture (200-1800m) as well as within the 300-1000 m range of most consistent catches. They were equally abundant in canyon and slope regions in the four seasons. The majority of the population inhabits bottom water deeper than 400 m and overlain by cold, well-oxygenated water.

Over 50% of all red crabs were larger than 96 mm CL (114 mm CW), the minimum size presently acceptable to processing plants. This proportion varied by sex, season and depth. Potentially marketable male crabs constituted 70% of total males caught, whereas less than 25% of females exceeded 96 mm CL. Seasonally the proportions were consistent for males, but varied for females. The proportion of large males was consistent over most of the depth range (200-1600 m). Most of the larger females were captured in water shallower than 600 m.

An inverse relationship between water depth and crab size was evident for females from 200-1500 m; for males only in the 200-500 m depth range. The mean size of males caught deeper than 600 m was fairly stable.

Females were more abundant than males in samples shallower than 600 m; males dominated catches in deeper water.

A spawning cycle is suggested although ovigerous females were captured in all seasons. Peak incidence of ovigerous females occurs in November characterized by a high percentage of late stage eggs and a peak incidence of recently extruded eggs. The

¹ Research cruises supported by National Science Foundation Grant GA-37561, J. A. Musick, principal investigator; by the University of Virginia Institutional Grant Program; and NOAA, Office of Sea Grant (NO. 04-3-158-49) for P.A.H. participation.

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ovarian cycle of non-ovigerous females complements the spawning pattern. From June through November, an increase in incidence of developing ovaries was accompanied by a decrease in advanced and mature ovaries. Absence of mature ovaries in November complements the peak incidence of ovigerous females at that time.

Relative density of red crabs was estimated for the Norfolk Canyon area and compared with values from other areas along the east coast of the United States.

INTRODUCTION

Interest in *Geryon quinquedens* Smith as a marketable species has been slowly increasing. Initial explorations (Schroeder 1959; McRae 1961) proved that red crabs were readily captured with trawls off the east coast of the United States. More recent surveys have been concerned with estimating fishery potential and evaluating harvesting methods, both in the United States (Gray⁴; Haefner and Musick, 1974; Ganz and Herrman⁵; Wigley, Theroux and Murray, 1975) and in Africa (Dias and Machado⁶; LeLoeuff, Intes and LeGuen, 1974; Intes and LeLoeuff, 1976). Technological and economic aspects of harvesting have also been under investigation (Varga, Dewar and Anderson, 1969; Meade and Gray, 1973; Holmsen and McAllister, 1974).

Other than the data obtained by Haefner and Musick (1974) and Wigley, et al. (1975), which were restricted to one period of sampling, observations on the biology of *Geryon* have been superficial. This paper supplements the survey of Haefner and Musick (1974) by presenting seasonal data on distribution, relative abundance and reproductive biology of red crabs in the Chesapeake Bight area of the western North Atlantic Ocean.

MATERIALS AND METHODS

Deep-sea red crabs were collected during demersal fish trawl surveys of Norfolk Canyon and an

adjacent open slope area in the Chesapeake Bight region of the western North Atlantic Ocean (Figure 1.) Four surveys, one in each season, were made during a period of three years using University of Miami vessels R/V *Columbus O. Iselin* and *James M. Gilliss* (Table 1). The sampling gear consisted of 15.1 m (headrope) semi-balloon, 4-seam shrimp trawls equipped with plastic mud-rollers and steel China V-doors. The nets were nylon of the following stretch mesh: 44 mm body, 37 mm intermediate, 36 mm codend and 12 mm inner liner. Thirty-minute tows were made in depth strata less than 1000 m; tow time was one hour at deeper stations.

Initially, an equal number of tows was to have been made in each of four depth strata (75-150 m, 150-400 m, 400-1000 m, 1000-2000 m) in the canyon and slope areas. Variations in actual depth of tows, encounters with bottom types prohibitive to trawling and cruise time limitations combined to alter the program. The realized effort is presented in Table 1. Mean trawl depths were calculated from depths recorded at start and finish and at 3-minute intervals during each tow.

All red crabs were processed at sea. Carapace width (CW, distance between the tips of the lateral spines) and carapace length (CL, distance from the diastema between the rostral teeth to the posterior edge of the carapace, along the midline) were measured to the nearest millimeter. The latter measurement was emphasized based on recommendations of Gray⁴. Accuracy in weighing, which was done aboard ship, depended on sea state conditions. In most cases, weight was recorded to the nearest gram; some larger specimens were weighed to the nearest decigram.

Females were examined for evidence of egg extrusion and hatching. Color of eggs was noted for most females. External eggs from selected ovigerous females were examined microscopically to relate developmental stage to egg color. Developmental stages of ovaries of selected non-

⁴ Gray, G. W., Jr. 1969. Investigation of the basic life history of the red crab (*Geryon quinquedens*). Rhode Island Div. Cons. Completion Rep. (P.L. 88-309, Proj. 3-46-R), pp.36.

⁵ Ganz, A. R. and J. F. Hermann. 1975. Investigations into the southern New England red crab fishery. Rhode Island Dept. Nat. Res. Div. Fish. Wildl. Mar. Fish. Sec. pp. 78.

⁶ Dias, C. A. and J. F. S. Machado. 1974. Preliminary report on the distribution and relative abundance of deep-sea red crab (*Geryon* sp.) off Angola, 8 p. In: Scientific papers presented to the second session of the International Commission for the Southeast Atlantic Fisheries (Madrid, December 1973), M. E. Bioceanol. Pescas, Angola, 12, pp. 75.

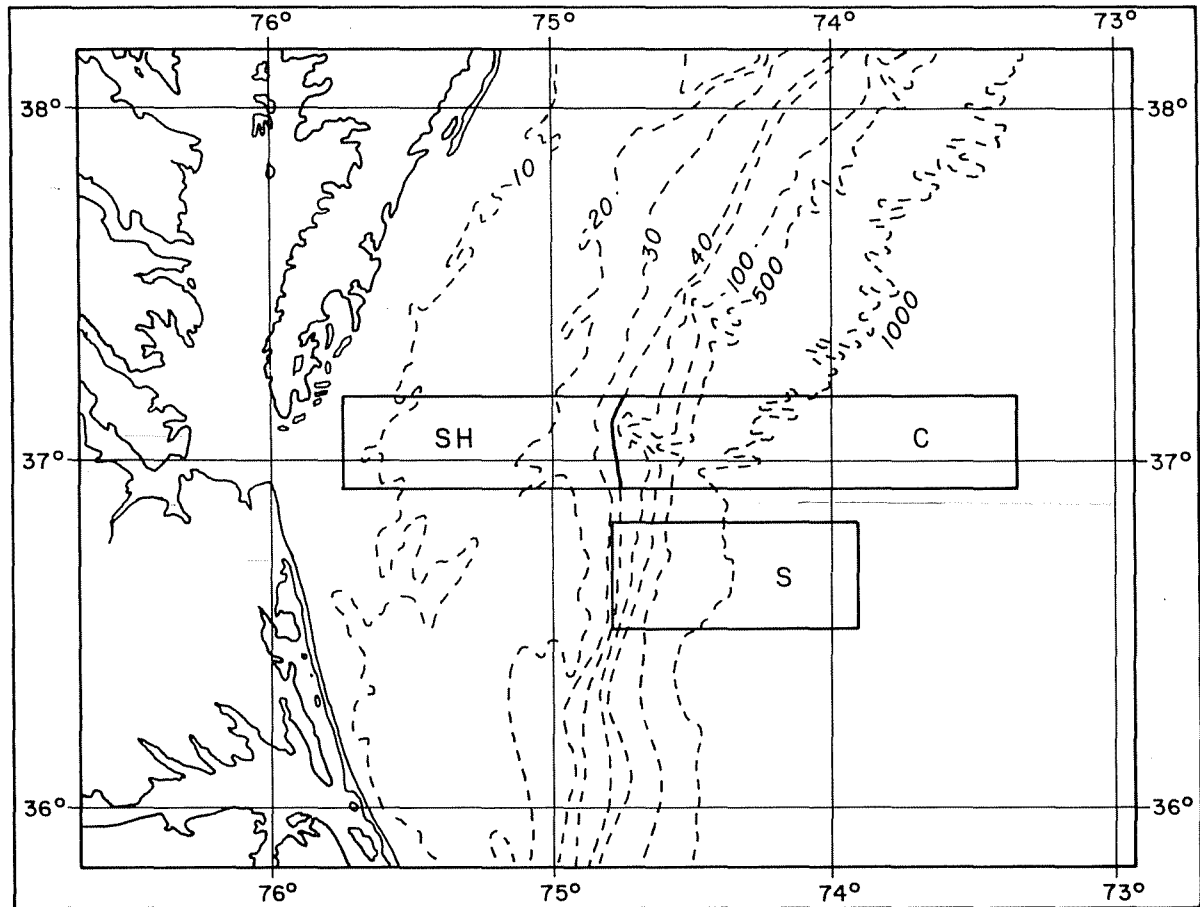


FIGURE 1. Chart of the Cheapeake Bight region of the western North Atlantic region showing shelf (SH), canyon (C) and open slope (S) trawl survey areas in the vicinity of the Norfolk Canyon. Isobaths in fathoms.

ovigerous females were classified as described in Haefner (1977).

Temperature and salinity of near-bottom water strata were monitored at trawl stations as well as at independent hydrographic stations. A variety of instruments was used including bathythermographs, expendable bathythermographs, a salinity-temperature depth recorder and reversing thermometers. Dissolved oxygen concentration of near-bottom water samples was determined by Winkler titration.

RESULTS AND DISCUSSION

Profiles of near-bottom (within 5-100 m of recorded depth) temperature and dissolved oxygen concentration (D.O.) for the four cruises are

presented in Figure 2. In all cases the data for canyon and slope areas are combined. The June plot reflects only data taken in conjunction with trawl stations; the other three plots include data from hydrographic and trawl stations. Only data from stations shallower than 1600 m are included.

Throughout the year temperature of near-bottom water was indirectly proportional to depth at depths exceeding 100 m (Figure 2). A large temperature gradient from 13°C to 6°C existed between 100 and 500 m. Below 500 m, temperature decreased gradually to 4°C at 1600 m.

Oxygen minima were associated with the thermal gradient (Figure 2). They were particularly obvious in June and November when D.O. values

TABLE 1. *Norfolk Canyon demersal trawl fishing effort, expressed as number of tows, in the canyon (C) and on adjacent open slope (S) by season and by depth strata between 200 m and 1800 m.*

Depth Stratum (m)	Spring		Summer		Fall		Winter	
	4-16 June 73		9-20 September 75		13-25 November 74		22-31 January 76	
	C	S	C	S	C	S	C	S
201- 300	6	1	3	1	1	2	2	2
301- 400	1	5	3	2	2	1	2	2
401- 500	1	0	0	0	0	0	1	1
501- 600	0	0	0	0	0	1	2	0
601- 700	1	1	2	2	3	3	0	1
701- 800	3	4	1	1	2	0	1	2
801- 900	0	0	2	1	0	1	1	1
901-1000	1	0	2	2	0	1	0	0
1001-1200	0	2	2	1	1	0	0	1
1201-1400	0	1	1	0	0	0	0	0
1401-1600	2	0	0	1	3	1	2	0
1601-1800	3	1	2	1	0	3	0	2
TOTAL	18	15	18	12	12	13	11	12

of 4.6 mg/liter were detected in near-bottom water within the 200-400 m depth range. Between 400 m and 800 m D.O. increased to 8 mg/liter, which persisted to a depth of 1600 m.

Except for shelf stations shallower than 200 m, salinity of near-bottom water was consistently between 35‰ and 36‰.

The 2539 red crabs caught during these cruises ranged from 16 mm to 143 mm in carapace length (CL). For purposes of comparing carapace length with carapace width (CW) reported in other papers, the following relationships were derived for 308 males, CL range 18-138 mm:

$$CW = 8.74 + 1.09 CL, r = 0.98$$

and for the 269 females, CL range 23-116 mm:

$$CW = 11.04 + 1.06 CL, r = 0.98$$

Male crabs attain a larger size than females. The largest male crab caught measured 143 mm CL and weighed 1200 g; the largest female was 123 mm CL and weighed 510 g. The following wet weight-length relationships were derived for 238 males ranging from 3 g to 1200 g:

$$\log \text{ male weight} = -3.58 + 3.14 \log CL, \\ r = 0.99 \text{ and for 142 females ranging from 4 g to 510 g:}$$

$$\log \text{ female weight} = -3.13 + 2.88 \log CL, \\ r = 0.97.$$

Although the size frequency distributions (Figure 3) indicate that the red crab is obviously not vulnerable to the trawl gear, certain modal groups (CL) were recognized in nearly every season. The most obvious were the 90-130 mm group for males and the 75-110 mm group for females. Other modal groups, such as 50-90 mm for males and 50-75 mm for females were less obvious. Wigley, Theroux and Murray (1975), in a survey extending from offshore Maryland north-eastward to Corsair Canyon on Georges Bank, observed similar modal groups for male crabs. Their female size frequency curve, however, did not indicate a well-defined intermediate group. On the other hand, their well-defined peak for red crabs less than 30 mm CL was missing from Norfolk Canyon samples.

Analysis of the Norfolk Canyon data using a three-point moving average, with subsequent calculation and plotting of percent cumulative frequency on probability paper was encouraging. Thirteen to fifteen smaller, less pronounced modes were detected which suggest molt classes within the larger modal groups. If, indeed, the smaller modes were representative of molt classes, a 6 to 11 percent range in growth increment (CL) is suggested. This range is comparable to four of the five

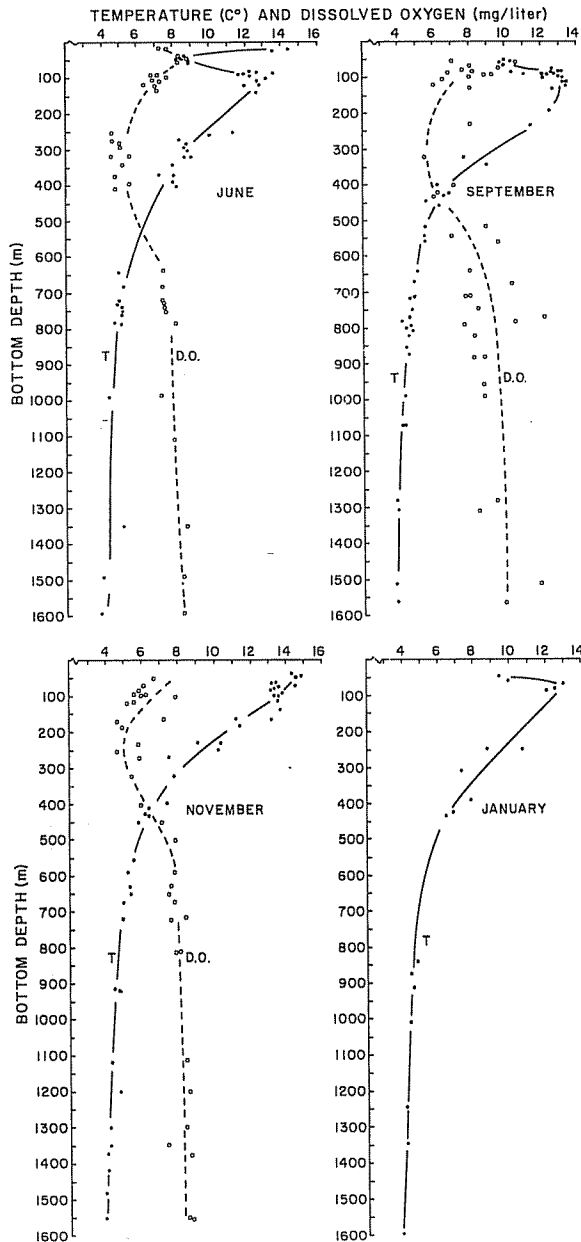


FIGURE 2. Seasonal profiles of temperature (T) and dissolved oxygen (D.O.) of near-bottom water in relation to depth in the Norfolk Canyon and adjacent shelf and slope area.

observations (6.7, 8.5, 8.9, 10.4, 18.1%) of Gray⁴ of crabs molting in the laboratory. One red crab molting at VIMS increased in length by 13.8%.

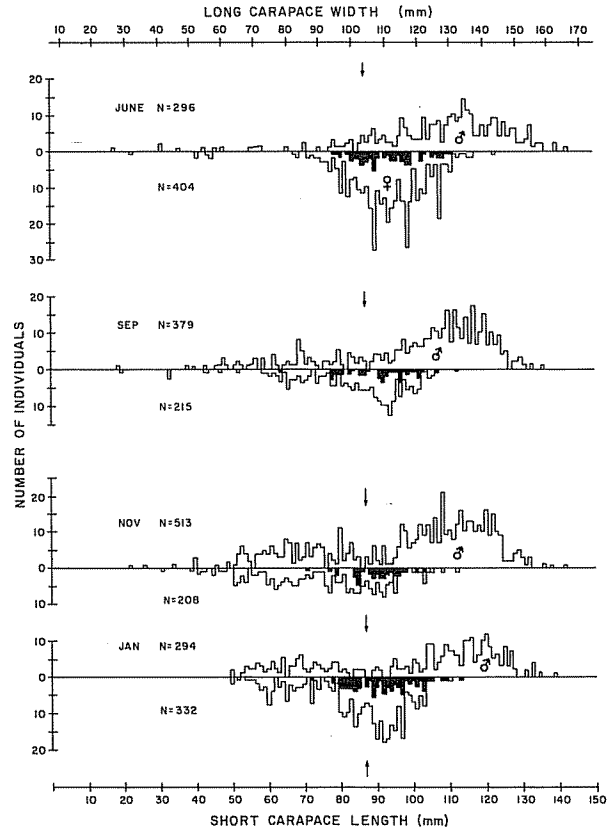


FIGURE 3. Seasonal size frequency distributions of *Geryon quinquedens*. Males are plotted above the line; females below. Black areas indicate ovigerous individuals and those with egg remnants on the pleopods.

Vertical arrows indicate present acceptable market size. Scales for carapace length and carapace width are included for comparative purposes.

Crabs less than 70 mm CL were poorly represented in the June sample (3% of the catch), but they made up an increasingly larger proportion of the catch through September (13.8%) and November (22.9%). The proportion in January (16.4%) was largely due to the absence of crabs less than 50 mm CL.

Over 50% of all Norfolk Canyon red crabs were larger than 96 CL (114 mm CW), the minimum size presently acceptable to processing plants (Wigley, Theroux and Murray, 1975). This proportion varied by sex, season and depth (Table 2).

Table 2. Number of Geryon quinquedens caught and percentage exceeding carapace length of 96 mm, arranged by depth and by season.

Depth (m)	JUNE				SEPTEMBER				NOVEMBER				JANUARY				TOTAL			
	Male		Female		Male		Female		Male		Female		Male		Female		Male		Female	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
201-300	0	0	0	62.5	65	27.7	1	0	0	0	0	0	0	0	0	0	9	55.6	65	27.7
301-400	115	94.7	288	44.4	21	90.5	59	33.8	13	92.3	23	26.1	19	84.2	13	53.8	168	92.9	383	42.0
401-500	12	100.0	32	75.0	0	0	0	0	0	0	0	0	72	84.7	182	19.2	84	86.9	214	27.5
501-600	0	0	0	0	0	0	0	0	31	90.3	17	11.8	35	65.7	87	22.9	66	77.3	104	21.2
601-700	36	72.2	7	14.3	136	63.9	32	9.1	228	72.3	87	5.7	21	61.9	4	50.0	421	69.1	130	8.5
701-800	117	67.5	84	11.9	14	71.4	4	0	165	40.6	54	1.9	54	84.9	8	0	350	57.7	150	7.3
801-900	0	0	0	0	44	90.9	10	10.0	17	64.7	3	0	86	32.6	39	0	147	53.7	52	1.9
901-1000	18	72.2	1	0	105	79.0	20	5.0	34	88.2	10	10.0	0	0	0	0	157	80.3	31	6.5
1001-1200	0	0	0	0	35	62.9	8	0	5	100.0	0	0	7	85.7	1	0	47	70.2	9	0
1201-1400	0	0	0	0	15	80.0	16	0	0	0	0	0	0	0	0	0	15	80.0	16	0
1401-1600	0	0	1	0	0	0	0	0	19	63.2	11	0	0	0	0	0	19	63.2	12	0
1601-1800	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
TOTAL	296	80.7	414	39.4	379	73.4	214	20.1	513	64.3	203	7.4	294	65.6	334	19.2	1482	70.2	1165	24.5

Potentially marketable male crabs constituted 70% of total males caught whereas less than 25% of the females exceeded 96 mm CL, a reflection of the larger ultimate size of male crabs. Seasonally, the proportions were consistent for males, but varied for females. A high proportion of females (39%) in June reflected the absence of small modal groups at that time; a low of 7.4% in November was related to a reduced modal group of large females.

These figures are markedly higher than the percentage (24%) of harvestable crabs in the northeast red crab survey (Wigley, Theroux and Murray, 1975). However, any comparisons between the two geographic areas must be qualified. Differences in size frequency distributions of the two populations are most likely related to the differences in sampling methods.

Comparison with other geographic regions is further complicated by difference in the acceptable harvestable size as well as in method of catch. For example, the minimum size of red crabs for the Ivory Coast of Africa is 84 mm CL (100 mm CW) (Intes and LeLeouff, 1976). In their survey 70% of the total catch of red crabs (38% of all males) was legal. If 84 mm CL instead of 96 mm CL was the accepted minimum market size in the United States, the percentage of potentially marketable male crabs caught in the Norfolk Canyon survey would increase from 70% to 78% and the percentage of marketable females would increase from 50% to 65%.

The proportion of large males in the population was consistent over most of the depth range (Table 2). Most of the larger females were found in relatively shallow water, <600 m.

The inverse relationship between water depth and crab size observed by Wigley, Theroux and Murray (1975) was also evident for females from 200 m to 1500 m and for males only in the 200-500 m depth range in the Norfolk Canyon region (Figure 4). The mean size of male crabs caught deeper than 600 m was fairly constant. Apparent seasonal variations shown in Figure 4 are due to lack of samples (Table 1) and/or low number of specimens in certain depth strata.

Red crabs were contagiously distributed within the Norfolk Canyon survey area within the total depth range of capture (220-1800 m), as well as within the 300-1000 m range of most consistent

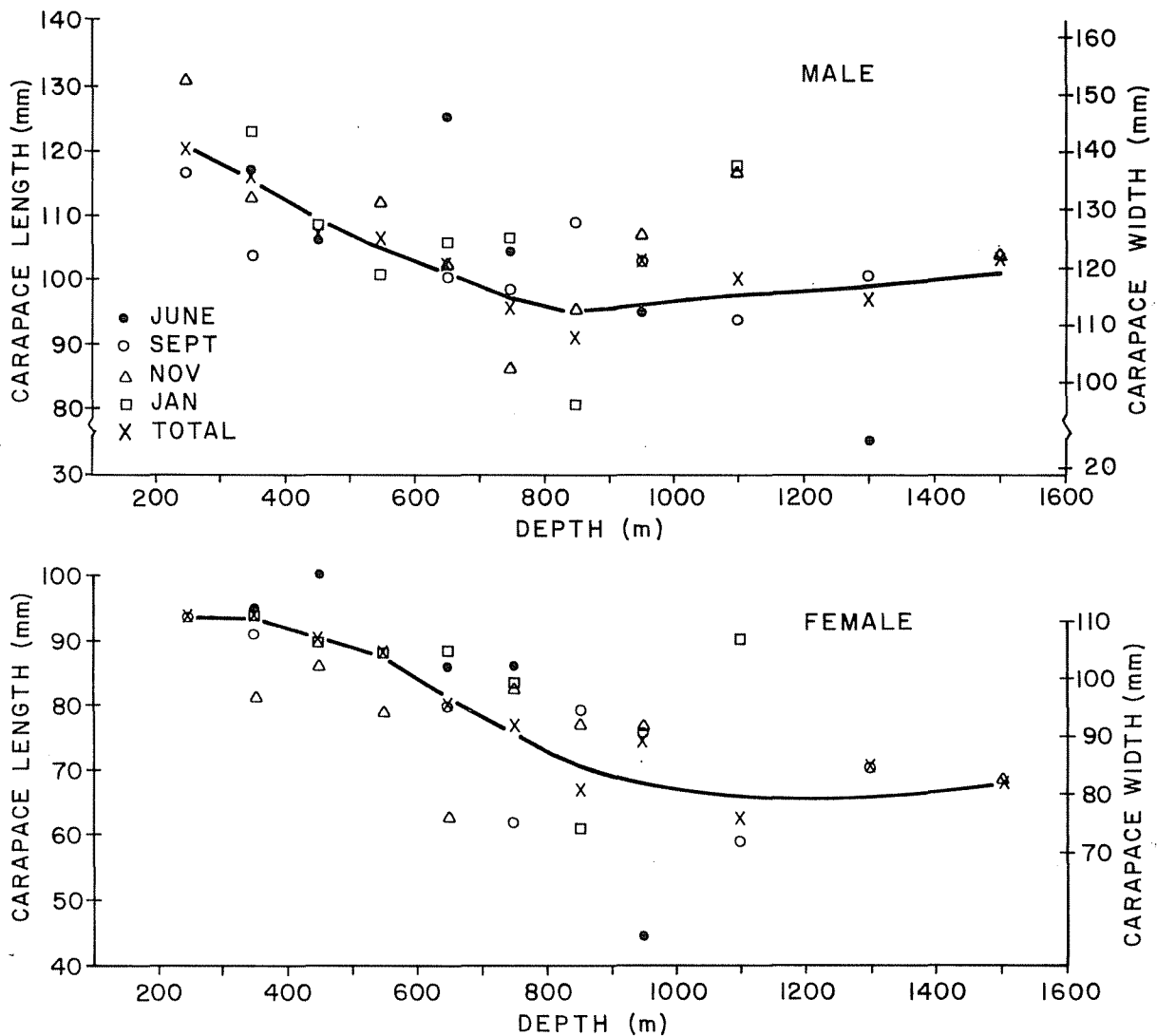


FIGURE 4. *Geryon quinquedens*. Relation of mean size of males and females to depth according to season and for all seasons combined. Scales for carapace length and width are included for comparative purposes.

catches. Because there was an excess of samples with zero catch and the variance exceeded the mean number of crabs per tow ($\bar{X} = 23.3$ within 200-1800 m; $\bar{X} = 39.5$ within 300-1000 m), catch data were transformed (Elliott, 1971) as an index of abundance: $Y = \frac{1+n}{n} (x+1)$ where x is the number of red crabs caught per 30 minute tow in any given stratum and n is the number of tows at any given depth. Data from the hour long tows were adjusted to correspond to half hour tows.

Red crabs were significantly ($P = 0.001$) more abundant on the adjacent slope than in Norfolk Canyon proper (Figure 5). Although stratifying depth by 100 m and 200 m intervals emphasizes voids in actual sampling depth (Table 1), it is evident that the distributional depth range is broad, from 200 to 1800 m (actual fishing depth range was 210 m to 1725 m). Most hauls were successful in catching crabs within the 400-1000 m zone (actual fishing depth 405 m to 1042 m) where relative

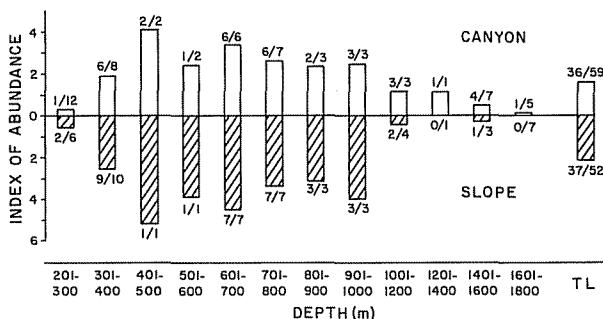


FIGURE 5. Relative abundance of *Geryon quinquedens* by area, expressed as index of transformed mean number of crabs per half-hour tow within each depth stratum. Fraction above or below each bar is the ratio of the number of stations at which red crabs were captured to the total number of stations in each stratum.

abundance was highest. The actual distributional depth range is most likely 210-1565 m because the single individual recorded for the 1601-1800 m stratum is suspected to be a wash-down from a previous sample.

In light of the temperature-dissolved oxygen-depth relationship, it is clear that the majority of the red crab population inhabits bottom waters deeper than 400 m which are overlain by cold, well-oxygenated water (Figures 2,5). A smaller percentage of tows caught crabs in the shallower (<400 m) areas where warmer, oxygen minimum water existed.

Females were more abundant than males in samples from depths shallower than 600 m; males dominated the catches in deeper water (Figures 6,7H). This segregation of the sexes by depth has

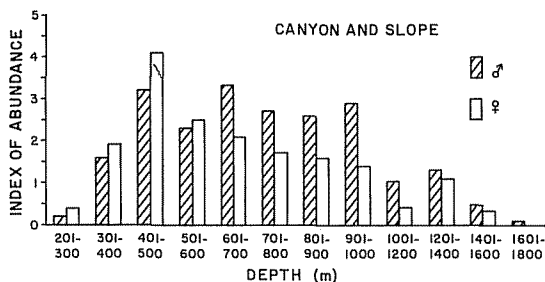


FIGURE 6. Relative abundance of *Geryon quinquedens* by sex, expressed as index of transformed mean number of crabs per half-hour tow within each depth stratum.

been observed in other areas. In Rhode Island waters Ganz and Herrman (1975) observed a lack of females between 700 m and 915 m; the greatest percentage of males was caught in 685-1110 m. The survey of Wigley, Theroux and Murray (1975) indicated a marked reduction of the number of females in water deeper than 500 m, where males predominated. Basically the same pattern was observed off the coasts of Angola

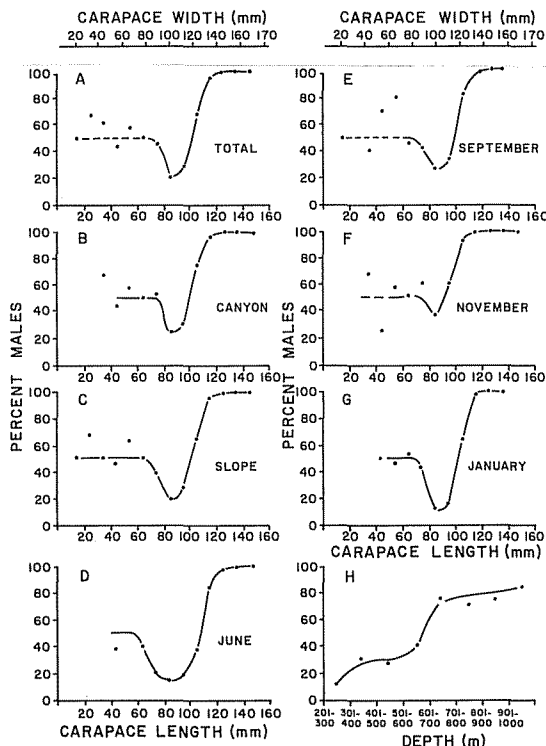


FIGURE 7. Percentage of Male *Geryon quinquedens* by size and depth. Data expressed as probability curves for total catch, area, season and depth. Scales for carapace length and width are included for comparative purposes.

(Dias and Machado⁶) and Abidjan (Ivory Coast) (LeLoeuff, Intes and LeGuen, 1974; Intes and LeLoeuff, 1976): the largest male catch was recorded from 600-700m; females were largely restricted to 300-400 m. A 400-600 m zone of transition was recognized wherein males and females occurred in variable, but nearly equal numbers.

The combined, four-cruise male: female ratio was 1.28:1, significantly different from the

theoretical 1:1 (Chi-Square, $P = 0.01$). The ratio varied from cruise to cruise with significant differences (M:F) in September (1.77:1), November 2.51:1) and June (0.73:1). The 0.88:1 ratio in January was not significant.

The presentation of sex ratio data in the form of probability curves (Wenner, 1972) is more meaningful. Red crab data were tabulated into 10 mm size classes and the sex ratio (as percent males) calculated within each class and plotted. The "anomalous" pattern shown for total red crab catch (Figure 7A) is not appreciably different than that for location (Figure 7B, C) or season (Figure 7D-G). Scatter about the curves is due to low numbers of individuals in the smaller size classes. The "anomalous" pattern is consistent with the Fisher theory (Wenner, 1972) in which a 1:1 offspring production is favored by natural selection, but a unique deviation from the 1:1 ratio is illustrated for older or larger animals.

The observed pattern is principally a function of physical size. The shape of the curve for red crabs exceeding 100 mm CL is determined by the larger maximum size of male crabs. Although growth rate and longevity are presently unknown for *Geryon*, it is known that females reach maturity at 65-75 mm CL, (Haefner, 1977) and continue to molt to eventually attain at least 116 mm CL. Males most likely reach maturity near 65-75 mm CL but attain a larger maximum size than females, either by more frequent molts, larger molt increments, living longer or by a combination thereof.

The paucity of males and an accumulation of females distributed about 85 mm CL (Figure 3) shows up as a dip in the probability curve. The accumulation of females in the large modal size group bracketing 85 mm CL could be due to longer intermolt intervals, smaller growth increments, terminal anecdyosis or inhibition of molting by vitellogenesis and spawning (oviposition). Such inhibition is known to occur in other crustaceans (Adiyodi and Adiyodi, 1970; Swartz, 1976).

The study of the reproductive biology of females was based on individuals exceeding 70 mm CL (85 mm CW), which includes most of the mature females (Haefner, 1977). This manipulation insures that most of the reproductively

mature segment of the female population is treated and reduces data bias due to variations in catch of smaller size classes. (Figure 3).

Wigley, Theroux and Murray (1976) related color of the external egg to developmental stage. Within the red-orange, brown, dark brown, purple and black spectrum, they judged newly deposited eggs to be light red or orange; eggs become darker as they ripen.

A microscopic examination of eggs from 11 extruded egg masses (sponges) from Norfolk Canyon crabs indicated a large variation in color within the earlier stages of development (Table 3). Because of the obvious difficulty in assigning specific development stage by color alone, the observed colors were grouped into early (A-C; orange-brown) and late (D; burgundy-purple-black) categories according to the scheme in Meredith (1952).

A spawning cycle is suggested for red crabs in the Norfolk Canyon area although ovigerous females were captured in all seasons (Figure 8).

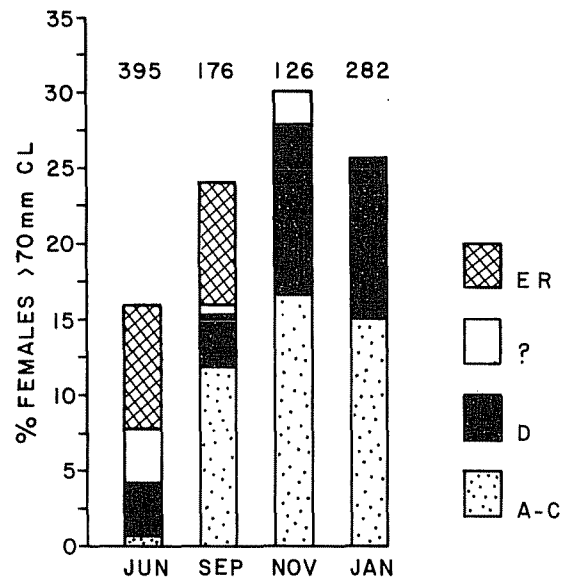


FIGURE 8. Seasonal percentage of early (A-C) and late (D) developmental stages of extruded eggs on ovigerous individuals and of egg remnants (ER) on total catch of female *Geryon quinquedens* >70 mm CL captured in the vicinity of Norfolk Canyon. Blank areas indicate unidentified egg stage. Sample size indicated by numbers above the bars. Egg stages are described in Table 3.

TABLE 3. *Developmental stages of external eggs of Geryon quinquedens. Size range based on measurements of 10 eggs from each sponge. Modified from Meredith (1952).*

Stage	Number of Sponges Examined	Description	Size Range (μm)	Color
B	7	Egg early to late blastoderm; nearly spherical. Minute eyes visible in larger embryos.	640-740	Orange Red-orange Red-brown
C	2	Eye $\frac{1}{3}$ - $\frac{1}{2}$ size of Stage D embryo; eye the only pigmented (brown) area. Yolk abundant. Abdomen free. Abdomen without melanophores.	710-780	Orange Red-orange
D	2	Pre-larval embryo. Eyes large. Abdomen and appendages well-developed, free from head. Red-brown pigmentation present, light over entire body, intense in eyes, cardiac and gastric regions of carapace, and in dorsal abdominal melanophores.	720-820	Burgundy Purple (black)

The presence of females bearing egg remnants and the low incidence of ovigerous individuals in June suggests a high incidence of egg hatching between January and June. This is based on the assumption that the presence of egg remnants indicates recent spawning. However, at the present time it is not known how long egg remnants remain on the pleopods. Hatching continues through the summer and is accompanied by an increase of ovigerous females bearing early stage (A-C) eggs. The peak incidence of ovigerous females occurs in November. This is characterized by a high percentage of females with late stage (D) eggs and a peak incidence of recently extruded (A-C) eggs. The percentage of ovigerous females in the population remains high in January, and although it is somewhat less than that observed in November, it is similar in the proportional makeup of early and late stage eggs.

Information on incidence and relative abundance of red crab larvae in plankton samples would help to resolve the presence or absence of a spawning cycle, but such data are presently unavailable or incomplete. Winter and spring samples off the coast of New Jersey have revealed very few first and second zoeal stages (P.O. Smyth, VIMS, personal communication). This indicates some hatching has occurred in winter and spring. Analyses of summer and fall samples are incomplete.

The ovarian cycles of non-ovigerous females (Figure 9) complements the spawning pattern. From June to September, there was no major change in ovarian stage. In November, an increase in the incidence of developing (intermediate) ovaries was accompanied by a decrease in advanc-

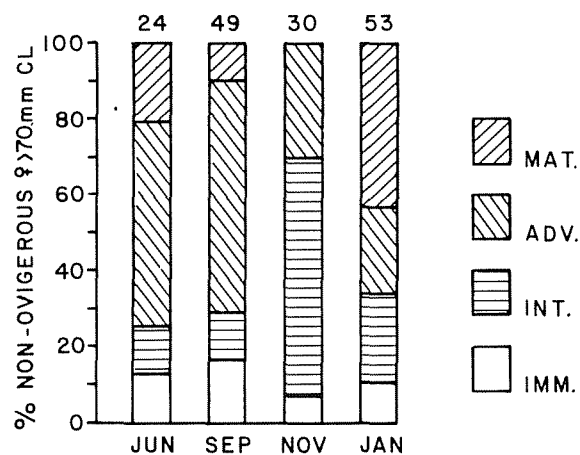


FIGURE 9. *Seasonal proportion of ovarian developmental stages (MAT, mature; ADV, advanced; INT, intermediate; IMM, immature) among samples of non-ovigerous female Geryon quinquedens >70 mm CL captured in the vicinity of Norfolk Canyon. Sample size indicated by numbers above the bars.*

ed/mature ovaries. The lack of mature (ripe) ovaries in November complements the peak incidence of ovigerous females at that time, suggesting that most of the mature females have extruded their eggs. Continued progressive development results in the higher proportion of advanced and mature gonads observed in January.

The temperature regime appears to determine the distribution of ovigerous females, the majority of which were captured in 400-800 m depths where temperatures exceeded 5° C (Figure 2.) Ovigerous females were captured over an extensive depth range in Norfolk Canyon although the evidence shown for the 1201-1400 m stratum is due to only two individuals in a small sample (Figure 10). The highest incidence of occurrence clearly fell within the 401-800 m depth range. Females with external eggs in early stages of development were found deeper than 300 m and were most frequently found within the 401-700 m depth range. The late

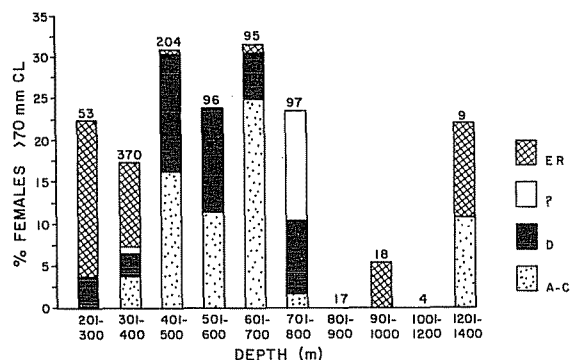


FIGURE 10. Depth distribution of ovigerous red crabs by egg development stage (A-C, D) and of females with egg remnants (ER) on pleopods, expressed as percentage of total catch of females >70 mm CL. Blank areas indicate unidentified egg stage. Numbers above the bars indicate number of females in sample. Egg stages are described in Table 3.

TABLE 4. Density of red crabs (no./hectare) captured by 13.7 m trawl and standing crop (in thousands of crabs) in vicinity of Norfolk Canyon (36°30'—37°10' N).

Depth (m)	September 1975		January 1976		All	
	No./ha	Crop 1000's	No./ha	Crop 1000's	No./ha	Crop 1000's
200-300	8.5	67.0	0	0	4.3	33.9
300-400	31.1	199.2	5.6	35.9	14.5	92.9
400-500	—	—	60.7	35.6	60.7	35.6
500-600	—	—	125.4	793.8	125.4	793.8
600-800	18.1	210.0	16.3	189.2	17.5	203.1
800-1000	23.6	337.3	51.4	734.5	30.4	434.4
1000-1200	8.6	162.5	14.4	272.1	9.2	173.8
1200-1400	31.9	703.7	—	—	31.9	703.7
1400-1600	0	0	0	0	0	0
1600-1800	0.1	4.9	0	0	0.1	4.9
All	13.2	2599.1	19.6	3859.3	15.8	3111.1

stage of development was most abundant at 401-800 m depth, but it was the only stage present in the 201-300 m depth stratum. Females with egg remnants were caught within an extensive depth range but were markedly more prevalent in shallower water (201-400 m) than in any other depth.

These data do, to a certain extent, corroborate the findings of Wigley, Theroux and Murray (1975) of an increase of spawning females with depth (to 640 m for their northeast sample), but there is no evidence from the Norfolk Canyon data to indicate seasonal differences in the incidence of early and late stage eggs with depth.

The presence of stage D eggs at 201-300 m (Figure 10) is due to September collections only and the high incidence at 701-800 m is due primarily to June collections. Only the females with egg remnants are restricted to two seasons, but the data for June and September (Figures 8, 9) are consistent with that shown in Figure 10. This preponderance of females with egg remnants in water warmer than 8° C (in June, they were captured in 300-400 m depth stratum) may not be coincidence. The migration of ovigerous females, with eggs in advanced stages (D) of development, into shallower, warmer water may enhance egg development and hatching. Although mortality of eggs and larval development as a function of temperature has not been determined, it is known that eggs survive and hatch at 15° C and larval development proceeds at temperatures as warm as 21° C (Perkins, 1973).

Relative density of red crabs was estimated for the September 1975 and January 1976 surveys (Table 4) when tow distances could be determined with reasonable accuracy from Loran C readings. Area fished was then computed from tow distance and the effective fishing width of the net, estimated to be 7.6 m (Haedrich, Rowe and Polloni, 1975). This accounted for 55.4% of headrope length, a value near the lower end of the range of values computed for other types of trawls (Griswold, Kurlyandsky and Twohig, 1971).

The relative densities were then used to compute standing crop estimates for the immediate fishing zone (Table 4). Area of each depth stratum within the zone was determined with a planimeter using a base chart constructed by E.P. Ruzewski (VIMS).

The relative densities of red crabs in the area of Norfolk Canyon were 50-95% lower than those observed for more northeasterly areas of the continental shelf and slope (Grassle et al., 1975; Wigley, Theroux and Murray, 1975) although a fair degree of overlap exists within the range of values of these three studies.

The low red crab density in the Norfolk Canyon area is most likely a reflection of the inefficiency of the collecting gear. The ineffectiveness of trawl nets in capturing contagiously distributed, motile megabenthic invertebrates has been revealed in certain gear comparison studies (R. Cooper and J. Uzmann, NMFS, personal communication). Ad-

mittedly, crab density calculations based on trawl catches are tenuous because of a number of variables (Wigley, Theroux and Murray, 1975). However, in order to compare their data with mine, I converted their trawl catches to relative densities (Table 5) and found that they fell short of the values determined by photographic sled. Their trawl densities, ranging from 19% to 78% of the

TABLE 5. Comparison of red crab densities determined by photographic sled and those computed for 4.9 m trawl for total geographic zone. Data source: Wigley, Theroux and Murray (1975).

Depth (m)	Red Crab Density		Percent of Sled Density
	Sled	Trawl	
229-320	21.1	16.5	78.4
320-412	258.3	190.2	73.7
412-503	273.2	136.5	50.0
503-640	282.0	53.8	19.1
640-914	91.4	45.5	49.8
914-1280	61.0	37.2	61.0
1280-1646	10.9	0	—

photographically estimated densities, were computed from an assumed vessel speed of 1.75 knots for a duration of 30 minutes, and an effective fishing width of 3 m for the 4.9 m (16 ft) trawl (Haedrich, Rowe and Polloni, 1975).

The small trawl is apparently more effective in capturing red crabs than is the large trawl. Although the larger net sweeps more than twice the area of bottom in a given unit of time, it is unable to capture twice the number of crabs, assuming the same density of crabs is available (vulnerable) to the gear. Although it is difficult to accept the apparent superiority of the 4.9 m trawl over the 13.7 m trawl in capturing red crabs (compare Tables 4 and 5), the fact is that it yielded larger catches on an equal effort basis (0-218, \bar{x} = 33; 0-197, \bar{x} = 23 crabs/30 minute tow, for small and large trawl, respectively). The relative ineffectiveness of the large net may be due to a number of factors such as lift of the net from the bottom and rolling over crabs in depressions. Net avoidance, however, is not likely a factor; a small net could be more easily avoided than a larger net.

There remains the possibility that the red crab stock in the Norfolk Canyon area may be relatively sparse compared with stocks distributed north-

easterly along the shelf and slope. This dilemma will not be resolved until the stocks are more effectively evaluated by tagging, gear comparison and calibration.

Other studies either cannot be compared to ours or to that of Wigley, Theroux and Murray (1975) because of variation in gear used (Schroeder, 1955, 1959). Furthermore, they present conflicting values. For example, Grassle et al (1975) determined red crab densities using photographic techniques in DSRV *Alvin*. Their values from two dives (180 crabs/ha in 495-499 m depth; 19.4 crabs/ha in 992-1000 m) represented 64% and 22%, respectively, of the photographic sled densities reported by Wigley, Theroux and Murray (1975) within the same geographic zone.

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