

Laboratory Growth, Reproduction and Life Span of the Pacific Pygmy Octopus, *Octopus digueti*¹

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ABSTRACT: *Octopus digueti* Perrier and Rochebrune, 1894 was reared through its life cycle at 25°C in a closed seawater system using artificial sea water. Two field-collected females produced 231 hatchlings: 193 hatchlings were group-cultured while 24 were isolated at hatching and grown individually to allow precise analyses of growth in length and weight over the life cycle. All octopuses were fed primarily live shrimps. Maturing adults fed at a rate of 4.7% of body weight per day and had a gross growth efficiency of 48%. Growth in weight was exponential for the first 72 days and described best by the equation: $WW(g) = .0405e^{.0646t}$. The mean growth rate over this period was 6.4% increase in body weight per day (%/d), with no significant difference between male and female growth. From 72 to 143 days, growth was logarithmic and described best by the equation: $WW(g) = (6.78 \times 10^{-6})t^{3.13}$. Females grew slightly faster than males over this growth phase. During the exponential growth phase, mantle length increased at a mean rate of 2.1% per day, declining to 1.1% per day over the logarithmic phase. No attempt was made to describe mathematically the period of declining growth rate beyond day 143. The primary causes of early mortality in group culture were escapes and cannibalism. Survival was good despite high culture density: 73% survival to date of first egg laying (day 111). Survival was better among the isolated growth-study octopuses: 88% to the date of first egg laying (day 130). Mean life span was 199 days in group-reared octopuses and 221 days in the growth-study octopuses. There was no significant difference between male and female life span. Progeny of the group culture were reared at similar stocking densities and fed predominantly fresh dead shrimp and crab meat. This diet resulted in cannibalism, with only 6% survival to first egg laying on day 128. Fecundity in this group was lower. *Octopus digueti* is a good candidate for laboratory culture and biological experimentation because of its small size, rapid growth, short life span, and good survival in group culture.

OCTOPUS DIGUETI PERRIER AND ROCHEBRUNE, 1894 is a small, benthic octopod inhabiting tidal flats in the northern Gulf of California (lat. 31°N, long. 114°W). *Octopus digueti* (Figure 1) shares several morphological and ecological characteristics with the Atlantic pygmy octopus, *Octopus joubini* Robson, 1929, and the Pacific blue-ringed octopus, *Hapalochlaena maculosa* Robson, 1929: similar adult size (20 to 60 g), large egg size (8 to 9 mm,

Figure 1), short life cycle (5 to 8 months at 25°C), and the habit of living within empty mollusc shells (Tranter and Augustine, 1973; Hanlon, 1983a; Hanlon and Forsythe, 1985). To date there is no published information on the biology and life history of *Octopus digueti*. We present here basic life cycle information that will contribute to ecological studies and to the evaluation of this species for use in laboratory culture and biological studies.

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MATERIALS AND METHODS

The closed culture systems and methodology are described in detail in Forsythe and

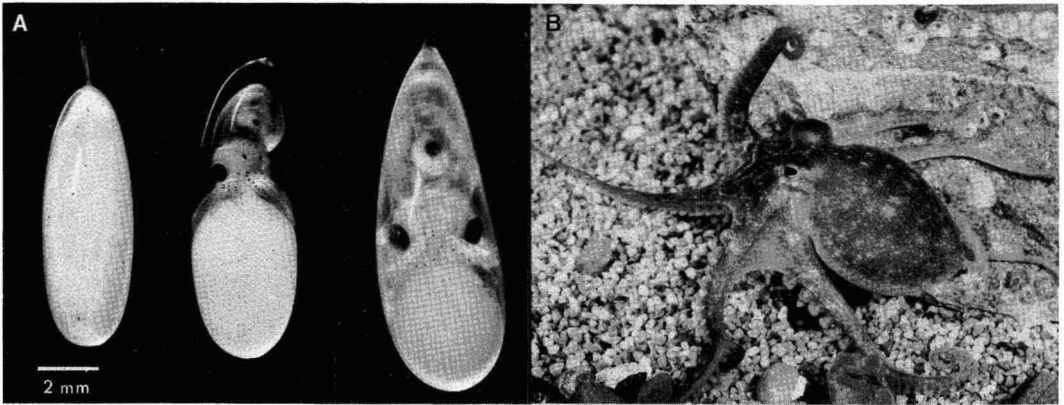


FIGURE 1. A. Embryos of *O. digueti* at three stages of development (25C): freshly laid, 3 to 4 weeks and ventral view at 5 to 6 weeks (immediately prior to the second reversal). B. An adult female *O. digueti* (ML approximately 5 cm).

Hanlon (1980) and Hanlon and Forsythe (1985). Briefly, the culture system consisted of a 2 m diameter circular fiberglass water-conditioning tank, 75 cm deep, of approximately 2000 l capacity and was the site of all water-conditioning processes. Two fiberglass culture troughs, 2.4 m \times 68 cm \times 30 cm, were supported on the upper rim of the water-conditioning tank and received freshly filtered artificial seawater (Instant Ocean[®]) continuously. All octopuses were cultured within these troughs.

Two female octopuses inhabiting mollusc shells (*Pecten* sp. and *Muricanthus* sp.) were collected in the northern Gulf of California near Puerto Peñasco, Sonora, Mexico. They were transported to the University of Arizona (Tucson), where they laid eggs in aquaria prior to shipment to Galveston. The brooding females were packed in separate plastic bags containing approximately 3 l of sea water and an equal volume of pure oxygen, then shipped by air to Galveston. Upon arrival they were placed directly into a culture system with the same temperature and salinity. A culture of *O. joubini* was in progress in the system at that time.

The two brooding females and their eggs were kept in separate plexiglass chambers (19 cm \times 14 cm \times 10 cm) with nylon screen sides (800 μ m), which allowed water circulation but prevented escape of hatchling octopuses. With the onset of hatching, hatchlings were

removed from the chambers daily, counted and placed into shallow (water depth, 3–4 cm) hatchling trays (50 cm \times 40 cm) within the main group culture troughs. One hundred ninety-three octopuses were placed into the group culture over a 23-day period. This group-reared population was provided with increased horizontal space as animal size increased, the first occurring on day 21 when half of the population was placed into a second hatchling tray.

Twenty-four hatchlings less than 15 hours old (nine from brood 1, 15 from brood 2) were isolated in individual growth chambers to allow precise measurements for a growth study through the full life cycle. The sides of the tightly lidded chambers (7 cm \times 5 cm) were replaced with fine nylon screen. The chambers were supported in the culture trough and supplied with strong water circulation. The octopuses were given larger dens and growth chambers as they grew.

Hatchlings in both the group culture and growth study were fed *ad libitum* on live mysidacean shrimps. As the octopuses grew, they were provided larger live foods, progressing from mysidacean shrimp (3–10 mm) to palaemonid grass shrimp (7–25 mm) to penaeid shrimp (2–6 cm). Crabs, fishes, and gastropods of appropriate size supplemented the shrimp diet.

Beginning at hatching, each animal in the isolated growth study was measured every 14

days. Measurements included: wet weight (WW), mantle length (ML) and total length (TL) (Forsythe, 1981; 1984). Dial calipers were used to measure length to the nearest 0.1 mm, and an electronic balance accurate to 0.01 g was used for all wet-weight measurements. To facilitate length measurement, the octopuses were narcotized for 90 to 120 seconds in a solution containing 1.5% ethyl alcohol and 1.5% ethyl carbamate in sea water. Excess water was removed by draining the mantle and blotting the epidermis with a moist paper towel. Octopuses were then weighed and manipulated as necessary for length measurements. All measurements required approximately 2 minutes total, after which the octopuses were returned to their chambers where they revived without assistance in 1 to 2 minutes. A random sample of 15 individuals from the group culture (over 10% of population) was weighed once per month starting on day 41. These animals were not measured for ML or TL so they did not require narcotization. Wet weights were taken by blotting excess moisture from the animal's epidermis with a moist paper towel and placing the octopus in a tared beaker of sea water on the balance.

For each chronological series of length and weight measurements, a line of best fit to the data was generated by least-squares linear regression and an equation describing the growth curve generated. The following equations were tested to generate lines of best fit to the growth data: linear, $y = a + bx$; exponential, $y = ae^{bx}$; and power, $y = ax^b$. In these equations $y =$ length or weight, $x =$ age in days, $a =$ the y intercept, $b =$ the slope and $e =$ the natural logarithm of 2. Length-weight and allometric growth relationships were examined using the above power function. Equations describing the best fit to these relationships were generated in the same manner as described above. Growth rates were calculated using the instantaneous coefficient of growth "g" calculated from the equation:

$$g = \frac{\ln Y_2 - \ln Y_1}{t_2 - t_1}$$

where Y_1 and Y_2 are lengths or weights at times t_1 and t_2 . Multiplying g by 100 gives the in-

stantaneous relative growth rate as percent increase in body size per day. Multiplying g by mean lengths or weights over the given time interval gives a growth rate as mm/day or g/day.

The food intake of six octopuses (2 males, 4 females) from the growth study group was measured over a 41-day period (days 97–138) to estimate feeding rates and gross growth efficiencies (GGE). Each octopus' daily ration of live shrimps was blotted dry and weighed to the nearest 0.01 g, while the previous day's food remains from that animal's chamber were collected and weighed. The amount of food ingested by each octopus was estimated by subtracting the weight of uneaten exoskeletons from the weight of the whole living shrimps; this amount was referred to as the ingested weight (IW). By dividing the ingested weight by the number of days in that interval, feeding rate was determined as grams of shrimp tissue eaten per day (g/day). Feeding rates were also calculated as percent of body weight (BW) ingested per day (%BW/day) from the equation: $\%BW/day = IW/WWt$, where t is the time period in days and WW is the mean wet weight during that time period (Choe, 1966; Mangold and Boletzky, 1973). Gross growth efficiency (GGE) was calculated over a given period by dividing the increase in wet weight of the octopus by the ingested weight and multiplying by 100 (Van Heukelem, 1976).

Since the octopuses in the growth study were reared individually, it was possible to compare males and females over the entire life cycle with respect to all growth data obtained. Comparisons of means of male and female growth data were examined using a t -test (Sokal and Rohlf, 1969: 200), after a variance ratio test (Zar, 1974: 101) was performed to assure that the means came from normally distributed populations. An analysis of covariance (Zar, 1974: 228) was used to test for differences in slopes and elevations of linear forms of calculated growth curves.

The progeny of the first laboratory-reared generation were group-cultured at a density equivalent to that in the first culture. From hatching, this group of octopuses was regularly fed both freshly killed and frozen foods

to evaluate the usefulness of such alternatives to live foods. Living octopuses were counted periodically to determine survival. No growth study was attempted with this group; however, all fatalities were weighed immediately after death.

RESULTS

Water Quality

Water quality in the transport bags containing females and eggs remained good during the 9-hour trip from Arizona to Texas. Only NH_4 levels were higher in the bags (0.7 mg/l) than in the culture system that they were transferred into. The exposure of embryos to temporarily high NH_4 levels had no obvious deleterious effects on development and subsequent hatching success. Water quality conditions in the culture system remained stable over the course of this study. Fluctuations were insignificant and of short duration. The mean temperature throughout the experiment was 24.9°C (range 21–27°C). Mean salinity was 35.2 ppt (range 33.0–37.5 ppt) and mean pH 7.9 (range 7.5–8.2). Biological filtration was effective: ammonia-nitrogen levels never exceeded the safe upper limit of 0.1 mg/l (Spotte, 1979; Hanlon and Forsythe, 1985), nitrite-nitrogen concentrations were consistently below 0.1 mg/l (with only one measurement recorded above this level), and nitrate-nitrogen levels exceeded 200 mg/l once (for 2 weeks), with the mean value being 117.9 mg/l (range 41.2–235 mg/l).

Hatching

Hatching occurred over a 23-day period resulting in a total of 231 hatchlings from both broods. Five dead embryos were found after hatching ended, while an additional nine hatchlings were apparently unviable and died within 24 hours after hatching. The modal hatching day was 10 days after first hatching. All of the growth-study octopuses hatched on the modal day. For standardization, the hatching day of the growth-study octopuses was considered day 1 for the entire experiment.

Foods and Feeding

Octopus digueti is an aggressive predator and will generally eat any crustacean, gastropod, fish, or other mollusc that is small enough for the octopus to subdue. Within hours after hatching they attacked and consumed live mysidacean shrimp of lengths exceeding their own. At 23 days (average WW approx. 0.2 g) they were able to kill and consume crabs with 2 cm carapace width, small palaemonid shrimps, and fish. When quantities of live foods of appropriate size were not available, pieces of finely cut fresh or frozen shrimp and crab meat were eaten as well. The octopuses showed a preference for live crabs, but ate live shrimp consistently as the primary diet. Fish and gastropods were eaten less frequently than shrimp when all were provided equally.

The mean feeding rate for six octopuses examined over a 41-day period beginning on day 97 on a live shrimp diet was 4.7% of body wet weight per day (Table 1). The mean feeding rate was 4.8%/d for females and 4.6%/d for males. Mean gross growth efficiency (GGE) was 48.1%. Mean male and female GGEs were the same. The range of GGE values from weekly estimations was wide (Table 1)—16.4% to 98.2%.

Growth

Growth measurements were taken every 2 weeks from hatching to day 169, by which time five of the 12 growth-study females had laid eggs. Each octopus was weighed immediately after death.

GROWTH IN WEIGHT: The growth-study octopuses increased from a mean wet weight of 0.04 g (range 0.03–0.06 g, $n = 21$) at hatching to an overall mean wet weight of 39.00 g (range 13.00–68.70 g, $n = 21$) at 169 days (Table 2). In comparison, mean wet weight at death for the 17 growth-study octopuses that died of natural senescence, from day 171 to day 258, was 28.3 g (range 7.7–44.9 g). At every weighing, mean female wet weight was greater than that of males. Mean female weight at 169 days was 44.13 g (range 18.45–68.70 g, $n = 13$) versus 30.68 g for males

TABLE 1

FEEDING RATES AND GROSS GROWTH EFFICIENCY (GGE) OF SIX GROWTH-STUDY OCTOPUSES. Feeding rates are given as percent of wet body weight ingested per day (%/d) and grams of shrimp tissue ingested per day (g/d). GGE is in percent (%). Combined (male + female), Male and Female data are given. On day 130 a female laid eggs and ceased feeding.

GROWTH INTERVAL (DAYS)	n		FEEDING RATES						GGE		
			(%/d)			(g/d)			(%)		
			MEAN	S.D.	RANGE	MEAN	S.D.	RANGE	MEAN	S.D.	RANGE
97-104	6	Combined	4.6	0.6	3.8-5.2	0.8	0.1	0.8-0.9	45.6	15.8	26.1-67.4
		Male	4.9	0.4	4.6-5.1	0.8	0.0	0.8-0.8	51.6	22.4	35.7-67.4
		Female	4.4	0.7	3.8-5.2	0.8	0.1	0.8-0.9	42.6	14.5	26.1-61.4
104-118	6	Combined	5.8	1.3	4.6-7.5	1.3	0.4	0.8-1.8	56.2	21.2	41.4-98.2
		Male	4.7	0.1	4.6-4.8	0.9	0.1	0.8-1.0	51.5	7.9	45.9-57.1
118-124	6	Female	6.3	1.3	5.0-7.5	1.6	0.3	1.2-1.8	58.6	26.6	41.4-98.2
		Combined	4.9	2.1	2.0-8.2	1.4	0.9	0.6-3.1	61.2	15.9	49.2-92.0
124-131	5	Male	5.4	1.3	4.5-6.3	1.2	0.2	1.1-1.4	57.3	5.9	53.1-61.4
		Female	4.6	2.6	2.0-8.2	1.5	1.1	0.6-3.1	63.2	19.8	49.2-92.0
		Combined	4.3	0.6	3.4-5.0	1.4	0.4	1.1-2.0	38.9	15.7	16.4-54.4
131-138	5	Male	4.4	0.3	4.2-4.6	1.2	0.0	1.2-1.2	52.4	2.9	50.3-54.4
		Female	4.2	0.8	3.4-5.0	1.6	0.5	1.1-2.0	30.0	13.8	16.4-44.0
		Combined	3.9	1.3	2.9-6.2	1.5	0.9	1.1-3.2	34.8	7.7	23.8-43.5
Overall values	28	Male	3.6	0.3	3.4-3.8	1.1	0.0	1.1-1.1	28.1	6.0	23.8-32.3
		Female	4.1	1.8	2.9-6.2	1.8	1.2	1.1-3.2	39.4	4.9	33.9-43.5
		Combined	4.72	1.4	2.0-8.2	1.3	0.6	0.6-3.2	48.1	18.0	16.4-98.2
	10	Male	4.59	0.8	3.4-6.3	1.0	0.2	0.8-1.4	48.2	13.7	23.8-67.4
		Female	4.80	1.7	2.0-8.2	1.5	0.7	0.6-3.2	48.1	20.4	16.4-98.2

(range 13.00-38.70 g, $n = 8$), a statistically significant difference ($p = 0.05$).

Growth rates were highest over the first 10 weeks (Table 2), with an overall mean of 6.41% increase in body weight per day (%/d), which produced a doubling in weight every 12 days. Growth was exponential and described best by the equation:

$$WW(g) = .0405e^{.0646t}; r^2 = .9993 \quad (1)$$

Males and females showed this same pattern of growth:

$$\text{male } WW(g) = .0381e^{.0648t}; r^2 = .9993 \quad (2)$$

$$\text{female } WW(g) = .0419e^{.0645t}; r^2 = .9992 \quad (3)$$

There was no significant difference between the slopes and elevations of growth curves for males and females.

Beyond 10 weeks, growth slowed and became logarithmic in form through day 143. Over this period, growth rates declined from 4.68 to 1.50%/d, with a mean overall growth rate of 3.02%/d. Growth over this period was

described best by the equation:

$$WW(g) = (6.78 \times 10^{-6})t^{3.13}; r^2 = .9885 \quad (4)$$

Equations for male and female growth were:

$$\begin{aligned} \text{male } WW(g) &= (2.47 \times 10^{-5})t^{2.82}; \\ r^2 &= .9857 \end{aligned} \quad (5)$$

$$\begin{aligned} \text{female } WW(g) &= (3.57 \times 10^{-6})t^{3.28}; \\ r^2 &= .9889 \end{aligned} \quad (6)$$

An analysis of covariance showed the slopes of male and female growth curves to be significantly different over this time period ($p < 0.001$). Thus, females were increasing in weight at a significantly higher rate than were males of the same age. During this period the overall growth rate for females was 3.1%/d compared to 2.8%/d for males. On a gram-per-day basis, females were growing at a mean rate of 0.58 g/d versus 0.39 g/d for males (Table 2).

The first appearance of the hectocotylus in

TABLE 2

GROWTH IN WET WEIGHT (WW) OF GROWTH-STUDY OCTOPUSES. At each measurement period the mean weight, standard deviation (s.d.) and range are listed for Combined (male + female), Male and Female data. Growth rates are given as % increase in body weight per day (%/d) and increase in grams per day (g/d). Doubling time is the number of days required to double in weight at the corresponding growth rate

	DAY	MEAN (g)	S.D.	RANGE	GROWTH RATE		DOUBLING TIME
					%/d	g/d	
Combined n = 21	1	0.04	0.01	0.03- 0.06	—	—	—
	15	0.11	0.02	0.07- 0.13	6.66	0.01	10.41
	29	0.25	0.04	0.19- 0.33	6.13	0.02	11.31
	43	0.69	0.14	0.52- 1.02	7.14	0.05	9.70
	58	1.79	0.37	1.29- 2.71	6.34	0.11	10.93
	72	4.00	0.71	2.95- 5.44	5.76	0.23	12.04
	86	7.70	1.50	5.66-11.22	4.68	0.36	14.80
	100	13.73	3.12	9.25-21.75	4.13	0.57	16.79
	114	19.51	5.24	10.88-31.18	2.51	0.49	27.64
	128	26.82	7.59	13.59-44.06	2.27	0.61	30.50
	143	33.57	10.76	14.43-55.66	1.50	0.50	46.29
	156	37.07	13.11	14.23-60.87	0.76	0.28	91.00
	169	39.00	15.15	13.00-68.70	0.39	0.15	176.97
Male n = 8	1	0.04	0.01	0.03- 0.05	—	—	—
	15	0.10	0.02	0.07- 0.12	6.81	0.01	10.18
	29	0.24	0.03	0.19- 0.28	5.88	0.01	11.79
	43	0.64	0.10	0.52- 0.78	7.15	0.05	9.70
	58	1.71	0.29	1.35- 2.14	6.54	0.11	10.61
	72	3.85	0.70	3.04- 5.03	5.79	0.22	11.96
	86	7.21	1.29	5.66- 9.07	4.47	0.32	15.49
	100	12.18	2.18	9.25-15.46	3.74	0.46	18.52
	114	16.53	3.37	10.88-21.70	2.18	0.36	31.75
	128	21.00	4.03	13.59-26.34	1.71	0.36	40.49
	143	27.07	7.13	14.43-37.36	1.69	0.46	40.96
	156	30.13	8.17	14.23-40.84	0.82	0.25	84.34
	169	30.68	8.14	13.00-38.70	0.14	0.04	498.04
Female n = 13	1	0.04	0.01	0.04- 0.06	—	—	—
	15	0.11	0.02	0.07- 0.13	6.57	0.01	10.55
	29	0.26	0.04	0.19- 0.33	6.27	0.02	11.06
	43	0.72	0.16	0.52- 1.02	7.14	0.05	9.70
	58	1.83	0.41	1.29- 2.71	6.23	0.11	11.12
	72	4.09	0.73	2.95- 5.44	5.73	0.23	12.09
	86	8.01	1.58	6.16-11.22	4.80	0.38	14.44
	100	14.69	3.29	10.60-21.75	4.33	0.64	15.99
	114	21.34	5.44	15.20-31.18	2.67	0.57	25.99
	128	30.40	7.09	18.72-44.06	2.53	0.77	27.45
	143	37.57	10.85	20.07-55.66	1.41	0.53	49.07
	156	41.34	13.98	19.18-60.87	0.73	0.30	94.33
	169	44.13	16.41	18.45-68.70	0.50	0.22	138.00

growth-study males on day 86 coincided with the time of transition from exponential to logarithmic growth. After day 143, growth ceased to be logarithmic in form. Between days 143 and 169, five females and two males of the 21 growth-study octopuses had negative growth rates due to senescence and egg

laying. The period of declining growth rate beyond the end of the logarithmic phase represented a substantial portion (35%) of the life cycle. No attempt was made to describe growth in weight mathematically beyond day 143.

Growth in the group-culture population re-

TABLE 3

GROWTH IN MANTLE LENGTH (ML) AND TOTAL LENGTH (TL) OF GROWTH-STUDY OCTOPUSES. Only the combined (male + female) data are given

MANTLE LENGTH								
	DAY	(mm)	S.D.	RANGE	GROWTH RATE		DOUBLING	
					%/d	mm/d	TIME	
Combined n = 21	1	5.37	0.47	4.10-6.00	—	—	—	
	15	7.50	0.43	6.45-8.30	2.39	0.18	29.03	
	29	9.68	0.49	8.80-10.50	1.82	0.18	38.11	
	43	12.96	1.02	11.20-15.70	2.08	0.27	33.25	
	58	19.50	1.76	17.20-23.80	2.72	0.53	25.47	
	72	24.10	1.72	20.48-27.50	1.52	0.37	45.73	
	86	29.25	2.73	25.00-33.00	1.38	0.40	50.17	
	100	38.76	2.84	33.80-43.40	2.01	0.78	34.47	
	114	43.44	3.84	37.20-50.20	0.81	0.35	85.11	
	128	49.46	4.62	40.00-59.00	0.93	0.46	74.78	
	143	52.71	5.92	43.00-65.00	0.43	0.22	163.02	
	156	56.95	7.23	40.00-71.00	0.59	0.34	116.53	
	169	57.62	8.91	40.00-74.00	0.09	0.05	774.28	
	TOTAL LENGTH							
		DAY	(mm)	S.D.	RANGE	GROWTH RATE		DOUBLING
					%/d	mm/d	TIME	
Combined n = 21	1	11.94	1.80	7.40- 14.15	—	—	—	
	15	19.10	2.52	14.15- 22.50	3.36	0.64	20.65	
	29	27.20	2.43	22.90- 30.80	2.53	0.69	27.44	
	43	39.85	3.76	32.80- 47.60	2.73	1.09	25.41	
	58	59.75	5.19	53.00- 74.00	2.70	1.61	25.66	
	72	75.31	6.08	64.30- 84.00	1.65	1.24	41.94	
	86	94.03	8.49	76.30-107.40	1.59	1.49	43.70	
	100	115.09	9.10	97.30-127.30	1.44	1.66	48.03	
	114	132.95	12.71	105.70-160.00	1.03	1.37	67.26	
	128	144.79	14.75	114.00-173.00	0.61	0.88	113.72	
	143	156.57	20.37	105.00-190.00	0.52	0.82	132.91	
	156	170.57	25.89	125.00-221.00	0.66	1.12	105.22	
	169	169.86	27.70	106.00-215.00	-0.03	-0.05	-2147.32	

sembled that seen in the growth study. The mean growth rate calculated from group culture subsample weights at days 41 and 72 was 6.4%/d. There was no statistically significant difference between growth curves of the group culture and the growth study in the exponential phase.

From days 72 to 156, growth slowed to the logarithmic form and growth rates declined from 5.6%/d to 0.6%/d, with a mean of 2.3%/d. Growth in the group culture was significantly slower than the growth study in the logarithmic phase, resulting in a lower mean wet weight at the age of spawning.

Crowding and the inclusion of dead foods in the group culture diet from day 86 contributed to this difference.

GROWTH IN LENGTH: Tables 3 and 4 summarize growth, growth rates and equations for mantle length and total length. Like growth in weight, growth in length was exponential from day 1 to 72 and logarithmic from day 72 to 143. With one exception (ML at day 100), mean growth rates for mantle length and total length dimensions were highest over the first 72 days (Table 3). Analysis of covariance showed no statistically significant

TABLE 4

OVERALL GROWTH RATES (%/D) AND EQUATION VALUES FOR GROWTH IN MANTLE LENGTH (ML) AND TOTAL LENGTH (TL) OVER THE TWO GROWTH PHASES. Only the y-intercept (a) and slope (b) values for the general equations are listed. The coefficients of correlation (r^2) are also given

EXPONENTIAL PHASE (DAYS 1-72) ML or TL = ae^{bt}					LOGARITHMIC PHASE (DAYS 72-143) ML or TL = $a + b^t$			
ML	GROWTH RATE (%/d)	a	b	r^2	GROWTH RATE (%/d)	a	b	r^2
Combined	2.11	5.31	0.0214	0.9962	1.11	0.152	1.19	0.9798
Male	2.08	5.32	0.0212	0.9958	1.01	0.261	1.07	0.9651
Female	2.13	5.30	0.0215	0.9963	1.17	0.111	1.26	0.9836
TL	GROWTH RATE (%/d)	a	b	r^2	GROWTH RATE (%/d)	a	b	r^2
Combined	2.59	12.5	0.0261	0.9928	1.04	0.754	1.08	0.9853
Male	2.64	11.9	0.0265	0.9912	0.94	1.088	0.99	0.9719
Female	2.57	12.8	0.0259	0.9935	1.09	0.614	1.14	0.9889

difference in the slope or elevation of the male and female growth curves over either growth phase. There was a sharp increase in mantle length growth rate between days 86 and 100 for both males and females (see Table 3), after which growth rates slowed. There was no such increase in growth rate for total length. The increase in mantle growth rate corresponded roughly with the time of sexual development in the growth-study octopuses (male hectocotylus development on day 86, first mating observations on day 88) and first egg laying (day 130).

LENGTH-WEIGHT RELATIONSHIPS: Since previous analyses of growth in weight and length had shown two different growth phases over the life cycle, the mantle length versus wet weight data corresponding to the measurement intervals from days 1 to 72 and 72 to 143 were evaluated separately. An analysis of covariance revealed a highly significant difference ($p < 0.001$) in the slopes of the length-weight (L/W) relationship over these two time intervals. The first phase was described best by the equation:

$$WW(g) = (2.54 \times 10^{-4}) ML(mm)^{3.03};$$

$$r^2 = .9971 \quad (7)$$

and the second phase (72-143 days) by the equation:

$$WW(g) = (1.04 \times 10^{-3}) ML(mm)^{2.61};$$

$$r^2 = .9946 \quad (8)$$

An analysis of covariance between male and female data showed no significant differences over either growth phase.

For the benefit of field studies where the age of an octopus is unknown, a single L/W equation from days 1 to 143 (Figure 2) was calculated:

$$WW(g) = (3.19 \times 10^{-4}) ML(mm)^{2.93};$$

$$r^2 = .9979 \quad (9)$$

ALLOMETRIC GROWTH: Post-hatching growth produced no dramatic changes in body shape or proportions, although subtle changes did occur. The slope of the L/W relationship is a general indicator of allometry in body shape (Simpson et al., 1960; Forsythe, 1984). A slope of 3.0 indicates isometric body growth, with length and weight increasing in constant proportion to one another. Significant fluctuations above and below 3.0 can indicate allometric growth and a change in overall body shape. Based upon this (equation 7), growth appears isometric during the exponential growth phase and allometric during the logarithmic growth phase, resulting in a greater increase in mantle length per unit increase of weight in the second phase.

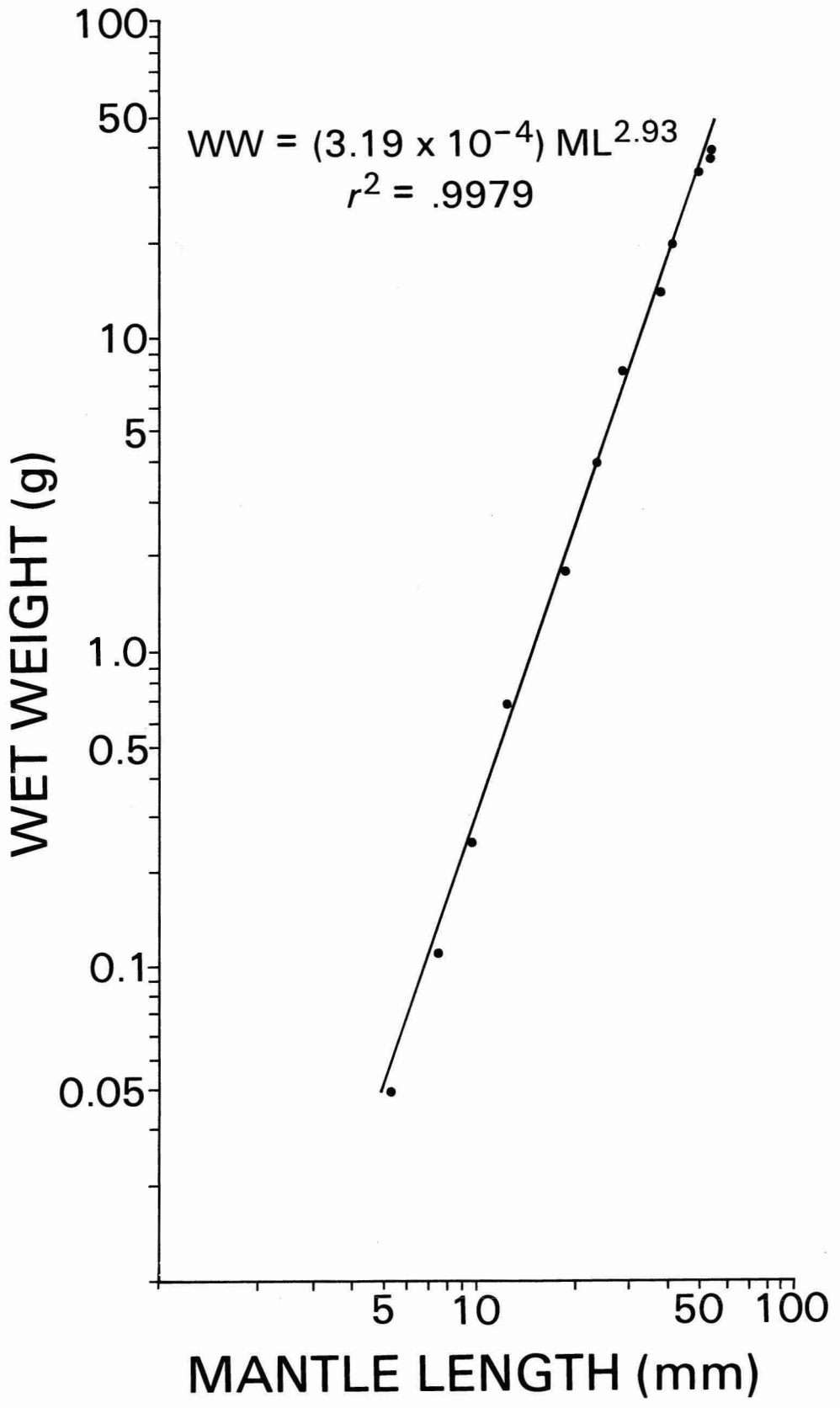


FIGURE 2. The overall (days 1 to 169) length-weight relationship for *O. digueti* taken from combined mean wet weight and mantle length data in Tables 2 and 3.

Linear body proportions changed slightly over the life cycle. In Figure 3, the percentage of total length represented by mantle length is plotted versus age. (Subtracting the mantle length percentage from 100% closely approximates arm length percentage.) At hatching, mantle length represented 45% of total length, but this percentage gradually declined to a low of 31% at day 86. Beyond day 100 the percentage stabilized near 34% ($\pm 1\%$). Using the power function, growth in mantle length was compared to growth in total length over both periods, with mantle length the dependent variable. The slope of this function is the constant of allometry. When the constant of allometry equals 1.0, growth of mantle length is proportional to growth in total length (i.e., isometric). While the L/W relationship was isometric during the exponential growth phase, linear growth was allometric as characterized by a constant of allometry of 0.817. This shows that total length was increasing in greater proportions to mantle length. This is substantiated by the higher growth rates in TL versus ML (Table 4) and agrees with the decrease in ML% in Figure 3. During the logarithmic growth phase, where the L/W relationship became allometric, linear growth had a constant of allometry of 1.1 indicating very slight allometry in favor of mantle length growth over total length. Mantle length growth rates are slightly higher than TL (Table 4) and it is during this phase that ML% increases from the low of 31% to nearly 34% (Figure 3).

Reproductive Biology

The first external sign of sexual maturation was the development of the male's third right arm into the hectocotylus (used for spermatophore transfer). Among growth-study males, it was recognizable on day 86. Matings in group culture octopuses were observed shortly thereafter on day 88. Mating style was consistent, with the mating pair fairly distant, often remaining in separate dens, and the male's hectocotylized third right arm stretched to span the distance. Matings were seen both day and night.

The first laboratory egg laying occurred in the group culture on day 111. Egg laying

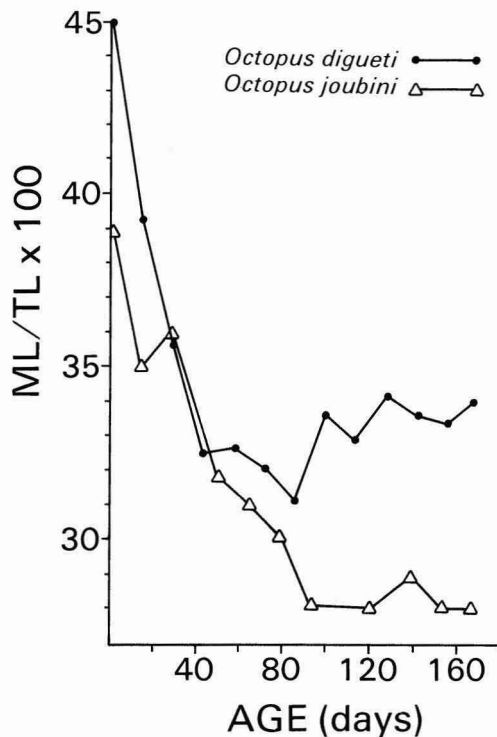


FIGURE 3. Allometric growth: change in mantle length as percent of total length over the life cycle for *O. digueti* and *O. joubini*. Data for *O. joubini* from Forsythe (1981).

began in the growth study on day 130 although no mating had occurred. Growth-study females were then paired with group-cultured males. Several of these males were killed by the females and no mating was observed. Primary egg deposits were small (fewer than ten eggs) and each egg was fastened individually to den walls. Egg laying in individual broods continued for 2 to 3 weeks, with final brood sizes ranging from ten to 125 eggs. Three females from group culture were isolated with freshly laid broods for monitoring egg development at 25°C (eggs taken for measurements were from these broods). Mean egg length (Figure 1) at laying was 7.9 mm (range 7.2–9.0 mm, $n = 15$). Mean egg width was 2.8 mm (range 2.6–3.0 mm, $n = 15$). Mean wet weight was 0.03 g. Eyespots (retinal pigmentation) became visible after 3 weeks at 25°C (Table 5) and the second reversal (Bolatzky, 1969) occurred at 5 weeks. After the second reversal, eggs were more sensitive to

TABLE 5

EGG DEVELOPMENT AND HATCHING OBSERVATIONS ON BROODS OF EGGS LAID AND MAINTAINED IN THE LABORATORY AT DIFFERENT TEMPERATURES

MEAN TEMP. (RANGE) (°C)	FIRST EYESPOTS VISIBLE	SECOND REVERSAL (d)	DEVELOPMENT TIME (d)	HATCHING DURATION (d)	PERCENT HATCHING SUCCESS	FEMALE'S ORIGIN	NO. EGGS
16.0 (13.5-18.5)	—	—	130	28	91	lab	13
16.0 (13.5-18.5)	—	—	133	30	100	lab	7
19.5 (17.0-22.2)	—	54	68	25	100	wild	100
19.9 (17.0-22.2)	—	53	62	30	100	wild	75
20.8 (19.5-22.3)	24	—	57	18	99	wild	142
21.1 (19.5-24.5)	—	—	57	13	100	wild	92
21.1 (19.5-24.5)	—	—	59	15	100	wild	18
21.1 (19.5-24.5)	—	—	53	13	100	wild	61
21.2 (19.5-24.5)	—	—	56	9	100	wild	94
21.2 (19.5-24.5)	—	—	53	16	—	wild	54
21.2 (20.0-22.3)	25	—	52	16	100	wild	100
21.2 (20.0-22.3)	23	—	52	12	100	wild	17
21.4 (19.5-24.5)	—	—	60	24	93	wild	59
21.4 (20.3-22.3)	—	—	56	27	100	wild	173
21.4 (20.0-24.0)	30	—	60	14	100	wild	79
24.9 (24.0-25.5)	—	—	50	16	100	lab	11
25.1 (25.0-25.8)	—	—	36	26	100	lab	125
25.3 (24.5-26.0)	—	34	41	29	100	lab	113

handling, so fewer eggs were measured. After the second reversal mean egg length increased by approximately 12% to 8.8 mm (range 8.1-9.6 mm, $n = 6$), mean egg width increased by 35% to 3.6 mm (range 3.3-4.1 mm, $n = 6$) and mean egg wet weight doubled to 0.06 g. Hatching occurred approximately one week after second reversal. Mean development time of those three broods was 42 days (range 36-50 days) at 25°C and mean hatching duration was 24 days (range 16-29 days).

The effect of temperature on the rate of egg development was dramatic (Table 5). The duration of egg development increased from a mean of 42 days at 25°C to a mean of 132 days at 16°C. The mean development times of 18 broods of *O. digueti*, laid and maintained in four different culture systems, were plotted against their respective mean temperatures. A line of best fit to the data was calculated by a least-squares linear regression resulting in the logarithmic equation:

Development time (days)

$$= (7.74 \times 10^4) \text{Temp } (^\circ\text{C})^{-2.35}; r^2 = .9010$$

Mortality

There was nearly 23% mortality in the first month of first generation group-culture (Figure 4). An actual count 8 days after hatching ended (day 21 of experiment) showed 22 octopuses unaccounted for (11% of stock population). Complete cannibalism or undetected escape are the only possible explanations for the missing animals. The remaining mortalities were due to cannibalism (4.6%), escapes (1.5%) and unknown causes (4.6%). Hatchlings were observed crawling 6 to 7 cm above the water line to escape; therefore after day 21, polystyrene lids were kept on the hatchling trays.

Overall mean survival in group-culture was 145 days (range 1-235 days). Seventy-three percent of the stock population (71 females and 70 males) survived to day 111, the first egg laying. Survival of brooding females beyond hatching was variable, but mean survival beyond final hatching of the three monitored females was 16 days (range 12-20 days).

Survival in the growth study was good.

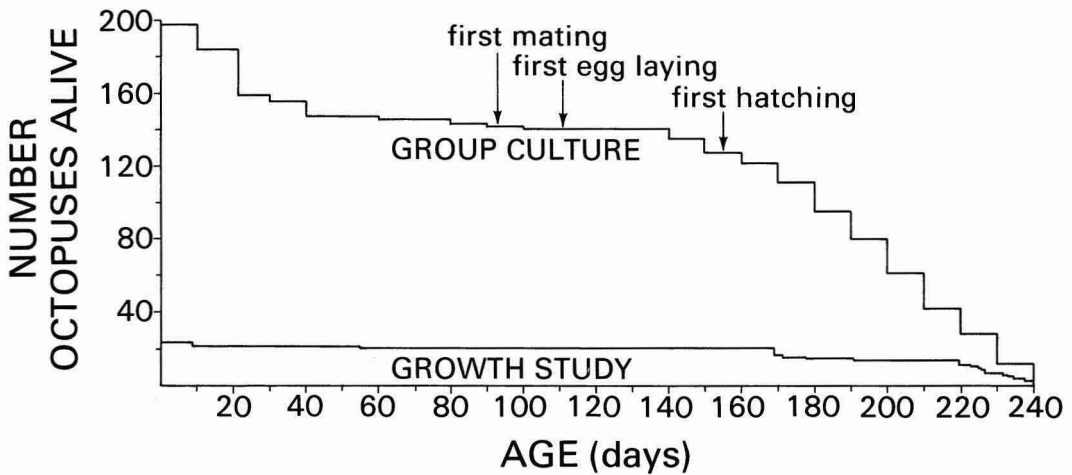


FIGURE 4. Survival of group-culture and growth-study octopuses.

During the second week, one octopus died without apparent cause and one was crushed trying to squeeze under its chamber lid. One more juvenile died while escaping on day 53. The remaining 21 octopuses (88%) lived beyond first egg laying (day 130) and into senescence (see below). Overall mean survival in the growth study was 192 days (range 9–258 days, $n = 20$).

Cannibalism and escape from culture trays were the primary causes of juvenile mortality, accounting for 17.5% of the entire first generation group culture in the first month (Figure 4). These two categories of mortality are combined since missing animals could have been either escapees or victims of complete cannibalism.

Aggression and cannibalism continued at lower levels throughout the period of sexual maturation, accounting for five of the seven deaths between days 34 and 118 involving both males and females.

Deaths caused by natural degeneration or senescence began abruptly in the group culture on day 125 and became the dominant cause of mortality. Senescent mortalities of males and females began at the same time.

Disease was not a significant cause of mortality. There were only ten deaths attributed to disease. This was surprising since they were sharing a tank system with a culture group of

O. joubini that had a lethal *Vibrio* spp. bacterial infection (Hanlon et al., 1984).

Senescence in females began with egg laying and brooding. Females stopped feeding abruptly from a week to several days before egg laying, after which they did not leave the den. They guarded and groomed their eggs throughout development and defended their broods vigorously. Prey organisms that blundered into the den were either repelled or killed, but were usually discarded uneaten. Without feeding, the females degenerated gradually, losing bulk, muscle tone and normal skin coloration. Brooding females usually survived through hatching, but there were some early deaths of brooding females and of females with unlaidd eggs. Males degenerated physically in the same way and at the same time as the brooding females; however, feeding activity in males decreased gradually over several weeks.

Second Generation Survival

Hatching of progeny from group culture octopuses at 25°C occurred over 53 days, with a total of 622 hatchlings from approximately 20 broods. Four hundred and three hatchlings were placed into one large group-culture tray (0.4 m²) as they hatched, and were fed primarily dead food (freshly cut palaemonid

shrimps). Day 1 for this generation was defined as the day of first hatching. Two hundred and nineteen octopuses were preserved upon hatching to control culture density. The first count of living octopuses was on day 33, after 321 hatchlings had been added to the group. There were 153 remaining or 48% of those added. Eighty-two fresh hatchlings were added to the culture group between days 33 and 46. By day 59 only 112 octopuses remained, 28% of the total. It appeared that older octopuses were cannibalizing younger animals, therefore the first hatching day was used to approximate the age of survivors rather than the modal hatching day of the entire population. Six percent of the population (11 females and 15 males) survived to the day of first egg laying (day 128). Only one of the three broods laid (all fewer than ten eggs) was observed to be fertile. All eggs were destroyed by the females or conspecifics shortly thereafter.

Life Span

Mortalities occurring after the onset of egg laying, within a study population, were attributed to old age or senescence if no other cause was apparent, and were used to approximate life span. Overall mean life span in the first generation group culture was 199 days (range 125–240 days, $n = 116$; discounting 15 animals used in experimentation and ten that were killed by conspecifics). Mean life span for females was 196 days (range 125–230 days, $n = 64$) and 203 days for males (range 136–240 days, $n = 52$). There was no statistically significant difference between male and female life span. Mean life span in the growth study was 221 days (range 171–258 days, $n = 17$). Mean life span for females was 218 days (range 171–258 days, $n = 9$) and for males it was 225 days (range 191–243 days, $n = 8$). Again, there was no significant difference between male and female life span. The difference in life span in the group culture (199 days) versus that of the growth study (221 days) was slightly significant ($p < 0.05$). The life span of the progeny from the first group culture population was 170 days (range 134–208 days, $n = 21$); mean age for females was 171 days (range 143–208 days, $n = 9$) and for

males was 169 days (range 134–204 days, $n = 12$). There was no significant difference between male and female data. At this time we can offer no clear explanation for the difference in life span of these three populations.

In evaluating the effect of reduced temperature on egg development, a dramatic increase in the life span of brooding females was observed. Two females from the first laboratory generation began laying eggs on day 170 and were moved to another system then gradually acclimated from 25°C to 16°C over several weeks. These two females would have been expected to live another 20 to 30 days at 25°C, however they both survived another 167 days (to day 338), dying within 24 hours of each other. It seems likely that life spans could exceed a year if animals were cultured at 16°C for the full life cycle.

DISCUSSION

Octopus digueti is now the third small octopus species for which there are laboratory data on growth, reproductive biology and life span. Similar information exists for *Octopus joubini* (Opresko and Thomas, 1975; Hanlon, 1983a; Forsythe, 1984) and useful, though less extensive, data have been reported for *Hapalochlaena maculosa* (Tranter and Augustine, 1973). Although found in three widely different water masses, these three species all have large eggs, benthic hatchlings, and grow to a maximum adult size of less than 80 g and 80 mm ML in under one year. Further comparisons can be made to other large-egged octopus species that grow to much larger adult sizes.

Comparisons of Octopus digueti, O. joubini and Hapalochlaena maculosa

In the following paragraphs where only two species are compared there are no comparable data for the third species. The feeding rates and gross growth efficiencies determined for *O. digueti* were typical of data reported for *O. joubini* and other octopus species (see reviews in Boyle, 1983; Forsythe, 1984) indicating *O. digueti* has comparable metabolic capabilities. Both *O. digueti* and *O. joubini* hatch at the same size and begin growing exponentially at

TABLE 6
LABORATORY DATA ON GROWTH, REPRODUCTIVE BIOLOGY AND LIFE SPAN FOR SIX SPECIES OF
LARGE-EGGED OCTOPUSES

	OCTOPUS DIGUETI	OCTOPUS JOUBINI	HAPALOCCLAENA MACULOSA	OCTOPUS BIMACULOIDES	OCTOPUS BRIAREUS	OCTOPUS MAYA
Temperature (°C)	25	25	20	23	25	25
Maximum Adult Size (g)	70	35	—	848	1100	5700
Hatching WW (mg)	40	40	—	70	95	100
Hatching ML (mm)	5.4	5.8	4.0	6.5	7.0	7.0
Overall Growth Rate (%BW/d) Exponential Phase	6.4	7.0	—	4.6	4.6	6.0
Overall Growth Rate (%BW/d) Logarithmic Phase	3.0	1.7	—	1.7	1.7	2.7
No. WW Doublings Exponential Phase	6.7	2.8	—	9.5	8.4	9.5
Size at End of Exponential Phase (g)	4.0	0.28	—	52	45	58
Duration of Exponential Phase (d)	42	28	—	142	140	105
Estimated life span (mo)	7	8	7	12	12	10
% Life Span in Exponential Phase (%)	36	12	—	35	39	35
No. Eggs/Brood	50–150	50–200	150	250–750	300–700	300–5000
No. Eggs/g of BW	2.0	5.7	—	0.85	0.63	0.88
Egg Length (mm)	7–8	6–7	6–7	10–17	12–13	11–17
Duration of Egg Development (d)	35–40	35–40	40–50	46–50	55–75	45
Egg Development as % of Life Span	18	15	21	13	18	15
References	Present study	Hanlon, 1983a Forsythe, 1984	Tranter & Augustine, 1973	Forsythe & Hanlon, 1988 & unpub. data	Hanlon, 1983b	Van Heukelem, 1976, 1983

similar growth rates (Table 6). The exponential phase is followed by a slower logarithmic phase in both species. The major difference in growth is the duration of the exponential phase: 72 versus 28 days, respectively. Both species have logarithmic phases with similar growth rates and duration, but *O. digueti* achieves four more doublings in size during its exponential phase than *O. joubini* (Table 6), thus *O. digueti* grows to a larger final size.

Mantle length growth rates are similar among the three species of pygmy octopuses being near 2.0%/d during the exponential phase and near 1.0%/d in the logarithmic phase (Forsythe, 1984). The durations of the growth phases again produce different growth patterns despite the similarities in growth rates (Figure 5). Because of its extended ex-

ponential growth phase, *Octopus digueti* has the largest mantle length of the three pygmy octopuses beyond hatching. The growth curves of *O. joubini* and *H. maculosa* parallel one another to day 60, with *O. joubini* slightly larger. The greater growth rate of *H. maculosa* produces larger mantle lengths than *O. joubini* beyond day 75 and a growth curve more closely resembling that of *O. digueti*. *Octopus joubini* maintains a nearly linear pattern of mantle length growth throughout its lifespan.

Growth analyses related to body shape and proportion yield quite different results for *O. digueti* and *O. joubini*. The slopes of the length/weight relationship are quite different throughout the life cycle. *Octopus joubini* weigh more than *O. digueti* of the same mantle length. The slope values suggest positive allo-

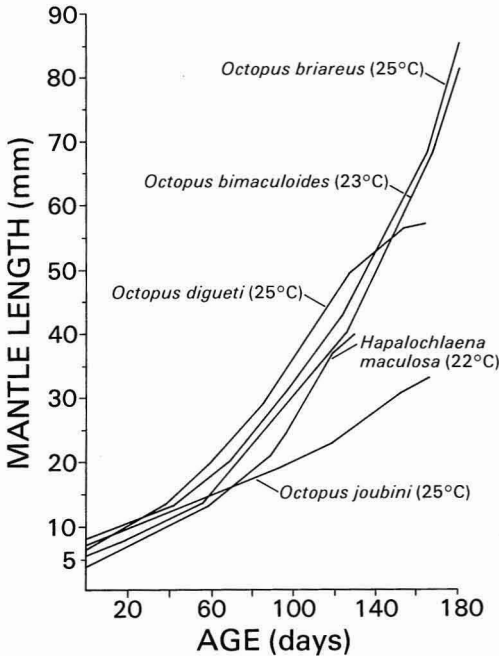


FIGURE 5. Mantle length growth up to 6 months of age for *O. digueti*, *O. joubini* (Forsythe, 1984), *O. bimaculoides* (Forsythe and Hanlon, 1988), *O. briareus* (Forsythe and Hanlon, unpub. data) and *Hapalochlaena maculosa* (Tranter and Augustine, 1973).

metric body growth (slope > 3.0) throughout the life cycle for *O. joubini* (Forsythe, 1984) versus early isometric growth followed by negative allometry (slope < 3.0) for *O. digueti*. Both species show a gradual decline in the mantle length's proportion to total body length (Figure 4) during the first third of the life cycle, meaning the arms are increasing in proportion to the mantle. This proportion stabilizes during the final two-thirds of the life cycle. However, *O. joubini* has a consistently shorter mantle length relative to total length (Figure 4), thus indicating it has longer arms than *O. digueti* of the same mantle length. Despite the differences suggested by the above observations, simultaneous observations of both species in this laboratory reveal that differences in overall body shape are not striking. *Octopus digueti* and *O. joubini* are very similar octopuses.

Strong similarities can be seen in most aspects of the reproductive biology of the

three species. *Octopus digueti* males develop a hectocotylus and begin mating at 3 months of age (25°C), while *O. joubini* (reviewed in Hanlon, 1983a) and *H. maculosa* (Tranter and Augustine, 1973) require another month at similar temperatures. Egg-laying also begins a month sooner for *O. digueti* than *H. maculosa* and *O. joubini*, although the latter species can spawn as early as *O. digueti* when reared at 27 to 29°C (Thomas and Opresko, 1973). Fecundity in all three species is very similar, although it is noteworthy that *H. maculosa* carries its eggs (Tranter and Augustine, 1973) while *O. digueti* and *O. joubini* both individually attach theirs to the walls of their den site. The duration of egg development in *O. digueti* and *O. joubini* is near 40 days at 25°C, and probably from 40 to 50 days at 22°C for *H. maculosa* (see Opresko and Thomas, 1975). *Octopus digueti* and *O. joubini*, like many other octopus species (Ambrose, 1981), show a negative correlation between water temperature and egg development time. Hatching duration is at least 1 to 2 weeks in all three species and can last up to 4 weeks in *O. digueti* and *O. joubini* (Hanlon, 1983a). At constant temperatures, hatching duration is almost certainly a reflection of the time span over which eggs are laid. For these small species, egg laying is apparently not a single rapid episode, but rather a gradual accretion over a relatively long period of time. A female *O. digueti* that lays eggs over a 3-week period has spawned for a period of time equivalent to 10% of its entire life span.

From laboratory growth studies it seems clear that all three of these small octopus species are capable of completing their life cycle in 6 to 7 months if temperatures remain above 20°C. Comparing animals reared individually at 25°C, *O. digueti* has a slightly shorter mean life span than *O. joubini*: 7 versus 8 months, respectively. At these temperatures, the maximal age attained by *O. digueti* has been 258 days versus 331 days for *O. joubini* (Forsythe, 1984). There is no difference in the life span of males and females in either species. Lower temperatures (16–20°C) can extend the life span of both species to approximately a year (this study; Hanlon, 1983a).

Comparisons To Larger *Octopus* Species

Forsythe (1984) concluded that *O. joubini*'s small size relative to larger octopus species was not due to slower growth, but rather its smaller hatching size and the shorter duration of its early exponential growth phase. The data for *O. digueti* further substantiate this observation. Compared to *O. bimaculoides*, *O. briareus* and *O. maya*, which grow ten times larger in weight, *O. digueti* grows faster in weight for the first 2.5 months of life (Table 6) and faster in mantle length for the first 4 months (Figure 5; no data for *O. maya*). However, its smaller hatching size and shorter exponential growth phase (Table 6) dictate its smaller final size. *Octopus digueti* achieves fewer doublings in weight during its shorter exponential phase (Table 6) ending up only one-tenth the size of the larger species. This ten-fold difference is maintained for the remainder of the life cycle where growth rates in the logarithmic phase are again comparable between species (Table 6). Interestingly, *O. digueti* shows a growth regime proportionally similar to the larger species (Table 6). Like the larger species, it grows exponentially between 30% to 40% of its life span before slowing slightly to a logarithmic growth phase. On this proportional basis, *O. joubini* remains somewhat unusual among octopuses in having such a short exponential growth phase, equivalent to only 10% of its life span. *Hapalochlaena maculosa* appears to have a growth regime intermediate to *O. digueti* and *O. joubini* based upon mantle length growth data (Figure 5). Small octopus species clearly have shorter life spans and therefore mature and spawn sooner than larger species grown at comparable temperatures (Table 6). On a proportional basis, however, differences are minimal. Males begin to mature at the end of the exponential growth phase, or about a third into the life cycle, and mating begins soon thereafter. Females remain immature throughout most of the life cycle, with the ovaries maturing rapidly just prior to spawning (Boyle, 1983). Of the species listed in Table 6, there is no significant difference in the life span of males and females. The small octopus species produce fewer and smaller eggs than large

species, but all yield benthic juveniles of similar behavioral and locomotor ability. Although absolute fecundity is lower, on a relative basis, smaller species appear capable of producing over twice as many eggs per g body weight than larger species. The duration of embryonic development is generally shorter in the small octopus species, but basically represents a comparable proportion of the life span in all six species (Table 6).

The data available for larger octopus species consistently show longer life spans at comparable temperatures. The species reviews of Boyle (1983) show life spans for larger octopus species to range typically from 12 to 18 months. Two species, *O. briareus* (maximum size 1 kg) and *O. maya* (maximum size 5 kg) can have life spans as short as 10 months at high temperatures (25–30°C). *Octopus bimaculoides* has a life span of 11 to 13 months at 23°C (Forsythe and Hanlon, 1988). It seems that small octopus species will thus produce more generations per year than larger co-occurring species growing under the same seasonal temperature constraints.

Nesis (1978) and Voight (1988) have suggested that *Octopus digueti* and *O. joubini* represent a geminate species pair that diverged from a common ancestor after the isolation of the tropical eastern Pacific Ocean from the Caribbean and Gulf of Mexico three to four million years ago. The remarkable similarities in most aspects of the biology and life history of *O. digueti* and *O. joubini* are consistent with such an evolutionary premise. Future development of genetic karyotyping methods for cephalopods may shed some light on these genetic relationships. Janet Voight, a graduate student in the Department of Ecology and Evolutionary Biology at the University of Arizona, has recently completed a one-year field study on the ecology of *Octopus digueti* at the same site where brood stock for this laboratory study were obtained. It will soon be possible to compare the growth, reproductive biology and life span of both field and laboratory populations of this species over the entire life cycle.

The range of biological experimentation that *Octopus* spp. have been used for (including *O. digueti*) was reviewed by Hanlon and

Forsythe (1985). The general anatomical and behavioral features of *O. digueti* most closely resemble *O. joubini*, another small species, and the convenient culture attributes and behavior of *O. digueti* render it suitable for many of the types of biological experimentation outlined previously (ibid.).

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