Growth of the Eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda)

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Abstract. *Loligo forbesi* Steenstrup is a commercially and biomedically important species ranging from Scotland to North Africa and from the Azores Islands in the central Atlantic east through the Mediterranean Sea and Red Sea. Eggs were collected from Plymouth, England and from the Azores and the hatchlings were reared to adult size in recirculating seawater systems. Growth data were obtained primarily from mortalities during the course of three culture experiments which lasted 360, 240 and 480 days. *Loligo forbesi* hatched at a size of 5–9 mg (3·0–4·6 mm mantle length, ML) and grew to a maximum size of 124 g (155 mm ML) in 413 days. In all experiments, growth was exponential in form for at least the first 3 months at rates of 5·8, 5·1 and 3·6% body weight per day (BW/d) at mean temperatures of 14·1, 14·0 and 13·1°C respectively. In one short-term experiment, month-old squids grew at 8·0% BW/d at 17·4°C. Growth beyond 3 months was slower and either logarithmic (as described by the power function) or exponential in form. Growth rates gradually declined to 1–2% BW/d. Analyses of mantle length growth confirmed the wet weight results. There was no evidence of sexual dimorphism in the laboratory populations, which were of small size, and the length–weight (L–W) relationships were found to be similar to those of field populations. Growth rates during the exponential growth phase appeared very sensitive to temperature, with a 1°C difference changing growth rate by 2% BW/d and producing a three-fold difference in weight at 90 days post-hatching. These dramatic effects of temperature on adult size and lifespan in nature are discussed. It is hypothesized that the small size of mature laboratory-reared squids was due to low culture temperatures during the first 3 months.

Introduction

Cephalopods are unique among multicellular organisms in their ability to sustain true exponential growth for a significant portion of their life cycle (Forsythe & Van Heukelem 1987). Years of fisheries studies have shown that squids, octopuses and cuttlefishes grow rapidly, but the existence of exponential growth remained hidden because this growth phase ended at a size below that sampled by collecting gear used in fisheries. Laboratory studies offer the only viable option for studying the growth of squids during their delicate early life stages. Exponential growth has now been demonstrated in numerous laboratory studies (Forsythe & Van Heukelem 1987), but few investigations have correlated the impact of such rapid growth on the life history of the species studied.

Loliginid squids are found world-wide and support major fisheries throughout their range (Roper, Sweeney & Nauen 1984). Fisheries studies have provided information primarily on adult populations of *Loligo* (e.g. Worms 1983; Rathjen & Voss 1987). Only recently have laboratory culture studies with loliginids shed light on younger stages (Yang, Hanlon, Hixon & Hulet 1980; Yang, Hanlon, Krejci, Hixon & Hulet 1983a; Yang, Hixon, Turk, Krejci,

Hanlon & Hulet 1983b; Yang, Hixon, Turk, Krejci, Hulet & Hanlon 1986). This paper analyses the growth of *L. forbesi* by focusing on squids cultured from hatching up to 480 days and comparing these data to available growth data from field studies.

Materials and methods

Loligo forbesi was reared from hatching through most of the life cycle in four laboratory culture experiments beginning in January 1983 and ending in February 1988; these are referred to as LF83, LF85 (LF85-1 in Hanlon, Yang, Turk, Lee & Hixon 1989), LF86 and LF88. Culture experiments LF83, LF85 and LF86 are chronicled in detail by Hanlon *et al.* (1989) and Yang, Hanlon, Lee & Turk (1989). Only a brief description of culture systems and methodologies will follow. All experiments were conducted in recirculating seawater systems ranging in size from 3500-l tanks for eggs, hatchlings and juveniles to 15000-l raceways for grow-out of juveniles to adult size. Natural seawater was normally used in the 3500-l systems while artificial seawater (Instant Ocean® brand) was used exclusively in the 15000-l systems. At hatching, the planktonic squids were fed a diet of wild, live zooplankton (primarily copepods) and small mysidacean shrimps (<7mm TL). As the squids grew, they received larger crustaceans and fishes. The squids received food 6–8 times per day between 0800 and 2200h. The first two experiments used eggs obtained from southern England (near Plymouth) and Roscoff, France (190km south of Plymouth) while the third experiment (LF86) used eggs obtained in the Azores Islands. For LF83 and LF86, eggs were laid by captive female *L. forbesi* while the LF85 eggs were collected in the field. In all cases, early stages (no eye spots) were shipped by air freight from the collection site to Galveston, where they were maintained at natural temperatures until hatching. Hatching occurred over 1–2 weeks in these experiments and the estimated modal hatching day was designated as experimental day 1.

Growth was measured as an increase in weight and length over time. Animals were placed on a dish and all excess water blotted away with absorbant tissue prior to weighing. Squids less than 0·05g were weighed to the nearest mg on a Mettler precision balance, while larger squids were weighed to the nearest 0·01g on standard electronic balances. After weighing, dorsal mantle length (ML) was measured to the nearest 0·1mm with dial calipers. The majority of data were obtained from measurements of daily mortalities. Weight data were taken only from freshly dead whole (intact) specimens, which represented only 6% of total recovered specimens. Only 14% of specimens were suitable for mantle length measurements. Data were obtained from live squids over the first 30 days post-hatching in the LF83 experiment and the first 50 days in LF88. In LF83, groups of 5–10 live squids were collected at approximately 7-day intervals. In LF88, squids were collected on days 1, 31 and 50. All squids were measured for weight and length and preserved for other analyses.

All measurement data from mortalities were summed into 5-day groupings beginning at day 1. The mean weight or lengths of these 5-day periods were then used in computer curve fitting procedures. The data were fit to the following equations: linear, $Y = a + bx$; exponential, $Y = ae^{bt}$; power (also known as logarithmic), $Y = ax^b$; and log, $Y = a + b\,lnx$, where Y = weight or length and x = age in days, a = the y intercept, b = the slope and e = the natural logarithm of 2 (Forsythe & Van Heukelem 1987). The square of the correlation

coefficient (r^2) was used to determine the equation best describing a given set of data. Growth rates were calculated using the instantaneous coefficient of growth, G, obtained from the equation:

$$G = \frac{\log_e Y_2 - \log_e Y_1}{t_2 - t_1}$$

where Y_2 = final weight or length, Y_1 = initial weight or length, t_1 = age in days at Y_1 and t_2 = age at Y_2 (see Forsythe 1984). The instantaneous relative growth rate (% increase in weight or length per day) was obtained by multiplying $G \times 100$.

Where necessary, data were compared using *t*-tests after variance ratio tests (Zar 1974) were performed to assure means came from normally distributed populations. An analysis of covariance (Zar 1974) was used to test for differences in slopes and elevations of linear forms of calculated growth curves. This was done using $\log_e(ln)$ transformed data.

Results

The four experiments were conducted sequentially in the same culture systems with similar maintenance and feeding protocols. LF83 was the most successful experiment with respect to the number of squids grown to adult size. Four hundred and thirteen animals reached an age of 6 months. Then a 72-h electrical stoppage in the aftermath of Hurricane Alicia resulted in the loss of approximately half of these animals. A large proportion of the survivors lived another 4–6 months to reach maturity. Many animals died of bacterial skin infections of the distal mantle tip during the last 2 months and this almost certainly shortened life-span. Water temperature was lowered from 16 to 13°C during this period in an attempt to retard bacterial growth in skin lesions. LF85 was the shortest experiment, coming to a premature end due to extensive bacterial infections of the mantle tip. At 6 months, temperatures were raised from 15 to 19°C in an attempt to accelerate growth, but apparently bacterial growth was also encouraged. The last 12 squids died on day 243 of toxic reactions to the antibiotic nifurpirinol (tradename Prefuran®) applied to the culture system water at a dosage of 0·2 mg/l active ingredient. LF86 was the longest squid culture experiment on record and lasted over 16 months. It also had the most stable temperature. LF88 was a small short-term experiment designed to test a hypothesis on the effect of temperature on growth rate of planktonic *L. forbesi*.

Experiments LF83, LF85 and LF86 show the same trend in survival, with 5–25% of squids surviving to day 30 and mortalities stabilizing thereafter. LF85 ended prematurely at 8 months, while LF83 and LF86 produced mature males and females with maximum life spans of 13 and 16 months, respectively. However, no spawning was achieved. LF88 was terminated at day 50 to measure the remaining squids.

After close scrutiny (Hanlon *et al*. 1989), the only variable between experiments that should have affected growth is temperature, which is summarized in Fig. 1. Each experiment had a different temperature pattern over its course. LF83 was near 14°C for the first 3 months, near 16°C for the next 6·5 months and then 13·2°C for the last 3 months. LF85 began low, averaging 13·2°C for 3 months, then increased to 14·8 for 3 months and up to 18·9°C for the last 2 months. LF86 was stable, averaging near 14°C throughout. LF88 began at 14°C for 17 days, raised 0·25°C per day for 13 days and held at 17·25°C for 20 days. The probable role of temperature in affecting growth will be brought out in the following sections.
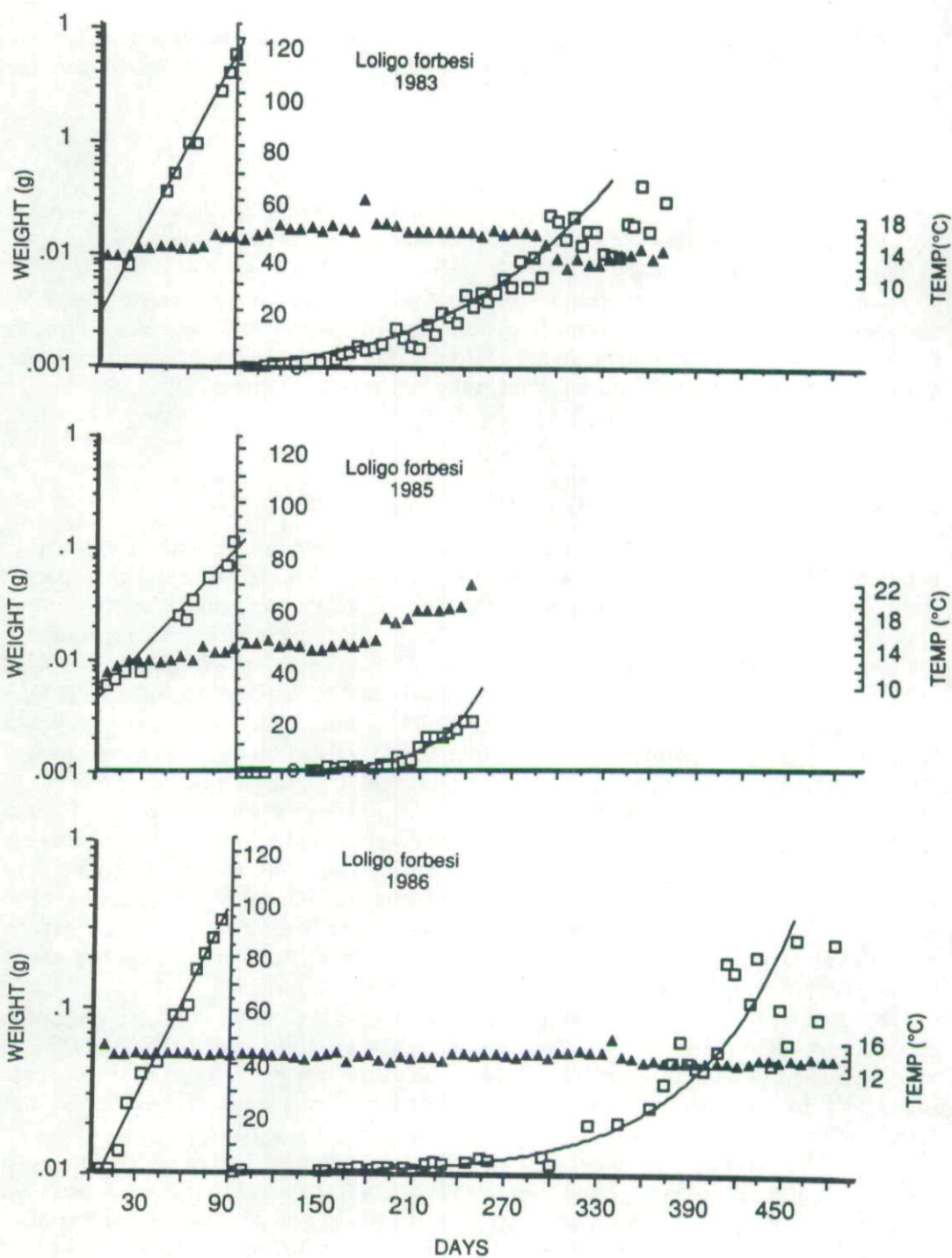
Figure 1. Growth of *Loligo forbesi* in three laboratory culture experiments. Open squares represent mean weight of squids over 5-day periods. Solid triangles represent weekly mean temperature. The first 90 days of growth are represented on a semi-log plot.

The four experiments provided over 9689 specimens of known age *Loligo forbesi*. From intact specimens, wet weight ($n = 528$) and dorsal mantle length ($n = 1352$) were recorded. In viewing the following analyses it should be remembered that, except where noted, the data were obtained from the daily mortalities of the culture experiments (with the cause of death rarely known) and not from healthy live squids. However, analysis revealed that mortalities reflected closely the living squid population in size.

Growth in weight

Table 1a summarizes these data. *Loligo forbesi* hatched at a weight near 5 mg and grew over five orders of magnitude to a maximum weight of 124 g in 413 days (LF86). The growth data

Table 1a. Laboratory growth in wet weight of *Loligo forbesi*. Data condensed into 30-day summaries (15 days each side of day shown). Growth rates calculated from measurement to measurement

Experiment	n	Age (days)	Mean weight (g)	SD	Range Min	Max	Growth rate (%BW/d)
LF83	23	31	0·03	0·01	0·01	0·05	–
	5	61	0·07	0·03	0·05	0·10	3·20
	17	91	0·56	0·21	0·29	1·02	6·80
	25	121	1·43	0·74	0·32	2·74	3·11
	9	151	4·70	2·46	2·00	8·59	3·97
	64	181	7·76	2·87	2·20	15·00	1·67
	16	211	13·95	6·83	4·94	34·17	1·96
	26	241	24·30	8·45	13·58	46·23	1·85
	37	271	34·44	11·62	12·69	60·05	1·16
	34	301	47·99	16·11	23·56	85·40	1·11
	20	331	47·91	12·49	29·65	87·46	−0·01
	13	361	59·57	13·41	42·26	88·49	0·73
LF85	19	20	0·01	0	0·01	0·01	–
	5	50	0·03	0·01	0·02	0·04	4·99
	10	80	0·12	0·05	0·05	0·20	4·50
	9	110	0·15	0·05	0·08	0·22	0·66
	7	140	1·29	0·63	0·46	2·39	7·21
	13	170	2·08	0·86	0·25	3·29	1·59
	10	200	8·28	5·15	3·06	17·80	4·60
	36	230	16·60	5·80	9·10	31·50	2·32
LF86	16	20	0·02	0·01	0·01	0·04	–
	8	50	0·09	0·03	0·05	0·17	5·81
	32	80	0·26	0·08	0·13	0·49	3·43
	2	110	0·39	0·11	0·31	0·46	1·30
	3	140	0·98	0·22	0·74	1·15	3·13
	9	170	1·50	0·49	0·68	2·30	1·41
	11	200	1·96	0·66	1·16	3·12	0·89
	10	230	3·97	1·72	1·97	8·08	2·35
	2	260	5·45	0·78	4·90	6·00	1·05
	2	290	5·51	2·14	4·00	7·02	0·04
	1	320	18·57	0	18·57	18·57	4·05
	2	350	22·40	3·96	19·60	25·20	0·63
	10	380	41·93	12·85	26·00	72·80	2·09
	9	410	58·75	28·01	28·20	124·30	1·12
	8	440	62·52	23·30	33·66	107·90	0·21
	5	470	77·15	22·26	45·50	106·00	0·70

analysed for each experiment (except LF88) are shown in Fig. 1. Linear assemblages of data on a semi-log plot define exponential growth, and in Fig. 1 it is evident that growth occurred exponentially over at least the first 90 days in all three experiments. The exponential functions described growth in weight over the first 90 days in each experiment are listed in Table 2. The y-intercept of all three functions falls in the 3–5-mg range, very close to actual hatching weight. An analysis of covariance revealed no significant difference in the y-intercept of these three functions. However, the slopes were all significantly different from

Table 1b. Laboratory growth in mantle length of *Loligo forbesi*. Data condensed into 30-day summaries (15 days each side of day shown). Instantaneous relative growth rates in % mantle length per day (%/d) calculated from measurement to measurement

Experiment	n	Age (days)	Mean length (mm)	SD	Range Min	Range Max	Growth rate (%/d)
LF83	153	15	3·50	0·64	2·00	5·00	–
	142	45	6·42	1·06	5·00	10·00	2·02
	49	75	15·33	3·17	8·00	20·00	2·90
	48	105	22·35	5·10	11·00	32·00	1·26
	13	135	29·77	3·61	24·00	36·00	0·95
	155	165	49·12	7·39	29·00	68·00	1·67
	21	195	52·90	6·21	40·00	65·00	0·25
	25	225	66·68	10·65	47·00	94·00	0·77
	41	255	82·20	12·29	68·00	117·00	0·70
	33	285	97·09	14·21	74·00	130·00	0·56
	28	315	107·46	11·70	80·00	128·00	0·34
	18	345	115·72	12·08	95·00	133·00	0·25
	4	375	131·25	6·18	124·00	139·00	0·42
LF85	138	18	3·08	0·55	2·00	4·00	–
	34	48	4·50	0·66	4·00	6·00	1·26
	29	78	8·66	1·78	6·00	12·00	2·18
	24	108	10·79	1·56	8·00	14·00	0·74
	12	138	25·42	3·73	21·00	33·00	2·86
	15	168	30·60	9·29	16·00	53·00	0·62
	8	198	45·13	9·96	32·00	62·00	1·29
	48	228	62·17	10·06	40·00	84·00	1·07
LF86	118	15	4·50	0·65	3·00	6·00	–
	30	45	7·63	1·12	5·86	10·00	1·76
	65	75	11·44	2·05	6·14	15·85	1·35
	21	105	15·46	1·76	11·50	17·90	1·00
	2	135	25·45	0·64	25·00	25·90	1·66
	12	165	27·06	4·35	19·60	33·80	0·20
	13	195	31·35	4·96	20·50	38·70	0·49
	10	225	40·78	7·45	27·90	51·70	0·88
	4	255	46·58	5·12	42·40	54·00	0·44
	2	285	45·00	7·07	40·00	50·00	−0·11
	1	315	66·45	0	66·45	66·45	1·30
	1	345	85·00	0	85·00	85·00	0·82
	10	375	90·40	15·42	75·00	127·00	0·21
	10	405	105·28	21·48	84·00	155·00	0·51
	7	435	110·03	16·70	86·30	135·50	0·15
	7	465	107·03	15·48	85·20	133·00	−0·09
	1	495	123·80	0	123·80	123·80	0·49

Table 2. Growth equations for wet weight, mantle length and the length/weight relationship. Data from measurements of daily mortalities unless noted otherwise

Experiment	Days	Wet weight (WW) equations	r^2	Equation
Post-hatching phase				
LF83 (live)	8– 37	WW (g) = $0.00489e^{0.0565t}$	0.9860	1
LF83	17–101	WW (g) = $0.00303e^{0.0565t}$	0.9922	2
LF85	5–243	WW (g) = $0.00416e^{0.0364t}$	0.9864	3
LF86	5– 95	WW (g) = $0.00570e^{0.0512t}$	0.9435	4
Juvenile to adult phase				
LF83	100–323	WW (g) = $3.69 \times 10^{-8} t^{3.68}$	0.9671	5
LF85	1–243	WW (g) = $0.00416e^{0.0364t}$	0.9864	6
LF86	95–400	WW (g) = $0.098e^{0.0155t}$	0.9650	7

Experiment	Days	Mantle length (ML) equations	r^2	Equation
Post-hatching phase				
LF83 (live)	8– 37	ML (mm) = $3.86e^{0.0178}$	0.9862	8
LF83	2–100	ML (mm) = $2.75e^{0.0199}$	0.9892	9
LF85	1–105	ML (mm) = $2.37e^{0.0149}$	0.9781	10
LF86	5– 95	ML (mm) = $3.36e^{0.0171}$	0.9841	11
Juvenile to adult phase				
LF83	100–323	ML (mm) = $0.0301t^{1.43}$	0.9760	12
LF85	90–243	ML (mm) = $6.44 \times 10^{-4} t^{2.105}$	0.9418	13
LF86	95–437	ML (mm) = $10.5e^{0.0057}$	0.9620	14

Experiment	Days	Length (ML) *vs* weight (WW) relationship	r^2	Equation
Post-hatching to adult size				
LF83	17–323	WW (g) = 2.94×10^{-4} ML $(mm)^{2.59}$	0.9847	15
LF85	5–243	WW (g) = 1.90×10^{-4} ML $(mm)^{2.80}$	0.9880	16
LF86	5–484	WW (g) = 2.99×10^{-4} ML $(mm)^{2.59}$	0.9945	17

one another ($P < 0.001$ in all cases). LF85 had the lowest slope value and lowest average temperature (13.15°C) over this period with a calculated instantaneous growth rate of 3.64% BW/d. At this rate, weight doubled every 19 days to yield 4.7 doublings over the first 3 months. LF86 had an intermediate average temperature (14.02°C) and an intermediate slope value; the growth rate was 5.12% BW/d with a doubling time of 13.5 days, or 6.7 doublings in 90 days. LF83 had the highest average culture temperature (14.13°C), slope value and growth rate (5.8% BW/d) with a doubling time of 12 days, or 7.5 doublings.

The single weight data set from live squids in LF83 compares well with the dead squid data (Table 2). Equation 1 predicts a live hatching weight (y-intercept) of 4.89 mg versus 3.03 mg from equation 2 (LF83 dead weight data), a reasonable difference when comparing the weight of a healthy living squid versus one found dead after some short period of starvation. The slope values are almost identical; thus the dead animal data closely reflect the growth of the living population.

It appears as though subtle differences in temperature (approximately 1°C) increased growth rate by approximately 2% BW/d (LF85 *vs* LF83). Starting with hatchlings of approximately the same size, the difference in exponential growth rate was magnified such that squids reared at an average temperature 1°C warmer were over three times larger at 90 days post-hatching (Fig. 1). The small LF88 experiment provided additional observations on the effect of increased temperature on the post-hatching growth rate of this species. The

experiment was begun and held at 14°C for the first 2·5 weeks then gradually raised to 17·25°C over the following 13 days. Over the first period growth rates were only 3·6% BW/d based upon combined measurements of live and dead squids (Table 3). From days 31 to 49, temperature remained at about 17·4°C and the growth rate was 8% BW/d. The last live squids were measured on day 49. The growth rate during the first 30 days was lower than expected; however, the dramatic increase in growth rate with a 4°C increase in temperature was clear.

For all experiments growth in weight beyond day 90 varied. In LF83, growth became logarithmic in form beyond day 100. Equation 5 in Table 2 was calculated to day 323. At this point in the experiment, temperatures were dramatically lowered (see Fig. 1) and growth plateaued. From days 90 to 323 growth rates gradually diminished from near 5% BW/d to near 1% BW/d (Table 1a).

In Fig. 1 the weight data for LF85 remain essentially linear throughout, thus suggesting continuous exponential growth. There was no reason to break the data at any one point, so a single equation was calculated for the entire data set (note that equations 3 and 6 in Table 2 are the same). The instantaneous relative growth rate remained near 3·5% BW/d throughout the experiment. This constant growth may be explained by the consistent rise in temperature over the course of the experiment. The average temperature over the first 3 months was 13·15°C, it was nearly 15°C over the next 3 months and almost 19°C over the last 2 months (Fig. 1).

Although temperature remained fairly constant (near 14°C) in LF86, growth distinctly changed after day 90 (Fig. 1). The data remained essentially linear but at a lower slope value up to day 400 when growth plateaued. An exponential function fit the data from day 90 to 400 slightly better than a power function (r^2 being 0·964 *vs* 0·946, respectively). Instantaneous growth rates declined abruptly in the 90–110 day range from near 5% BW/d before day 100 to just under 2% BW/d at day 120. However, instantaneous growth rates calculated from day 90 out to successive mean weights remained stable between 1·4 and 1·7% BW/d out to day 400. Again, the effect of temperature on the second phase of growth can be seen by comparing growth rates from days 100 to 250 in LF83 and LF86. A fairly steady difference of 2°C (16 *vs* 14°C, respectively) produced a difference in growth rate of 1% BW/d (2·4 *vs* 1·4% BW/d, respectively).

In all three experiments, hatching occurred over a relatively short period of time (1–2 weeks); however, significant size differences among siblings became apparent by the end of 3 months. By day 100, up to two-fold differences in weight among dead squids were seen in all

Table 3. Growth in weight of *Loligo forbesi* in experiment LF88. Measurements are from dead squids except those marked *, which were live animals sacrificed for measurement

Temperature (°C)	14	14	14·6	15·3	17·3	17·4
Culture day number	1	7	21	24	31	49
Mean WW (g)	0·0067	0·009	0·016	0·013	0·020	0·087
Ranges	0·006	0·006	0·012	0·011	0·016*	0·057*
	0·006	0·008	0·020	0·011	0·017	0·085*
	0·006	0·010		0·012	0·018	0·095*
	0·006	0·010		0·017	0·022	0·097*
	0·007	0·011			0·024	0·111*
	0·007				0·027*	
	0·008					
	0·008					

three experiments. The greatest observed size difference was in LF85 at day 158 (13-fold, 0·25 g *vs* 3·29 g). The greatest size difference observed in LF86 was 1·97 g *vs* 8·08 g at day 228. LF83 showed the greatest consistent size variation beyond day 100. Size variations of two-fold or more were seen regularly between days 100 and 300, the greatest being seven-fold at day 165 (2·2 g *vs* 15·0 g) among the hurricane mortalities. Beyond day 300 differences were often from 1·5- to two-fold. Obviously feeding differences account for these large variations.

Male and female growth data were analysed for LF83 and LF86 only. Separate analysis found no statistically significant difference in weight of males *vs* females at any point in the life cycle.

Growth in length

The mantle length data were analysed in the same fashion as the wet weight data. The data are summarized in Table 1b, while the regression equations fit to the data are given in Table 2 (equations 8–14). The length data were found to reflect the weight data in nearly all respects. In both LF83 and LF86, growth was exponential for the first 90–100 days, with LF86 changing to slower exponential growth out to day 400, while growth in LF83 became logarithmic in form to day 323. The mantle length data from LF85 differed from the weight data in that growth was exponential only to day 90. Over the first 3 months, as with weight, LF83 had the highest growth rate, LF85 the lowest and LF86 intermediate. There was no significant difference in the slope or elevation of the LF83 live data set from the LF83 or LF86 dead data (equations 8 *vs* 9 and 11 in Table 2).

Growth in mantle length beyond day 90 again mirrored the wet weight data by being of the same form and duration except for LF85 where a power function provided a better fit to the data. Squid growth is often reported in mm/mo for field data and Table 4 gives mantle length growth rates in mm/mo for each experiment over 90-day intervals. Beyond 6 months of age, the fastest growing animals were typically growing at over 10 mm/mo.

Analyses of male and female data (LF83 and LF86 only) found no statistically significant differences in size between sexes at any point in the life cycle. The length–weight relationship was analysed for all three experiments. Initially, equations describing the L–W relationship were calculated for the first 90 days and then from 90 days onwards, since the separate weight

Table 4. Mantle length (ML) growth rates for *Loligo forbesi* calculated from laboratory growth data. Growth rates (GR) are calculated in mm/month over successive 90 day periods beginning at hatching. Mantle length values were calculated from growth equations 9–14 in Table 2

	Experiment								
	LF83			LF85			LF86		
Time period (days)	Initial ML	Final ML	GR mm/mo	Initial ML	Final ML	GR mm/mo	Initial ML	Final ML	GR mm/mo
1– 90	2·8	17	4·7	2·4	9	2·0	3·4	16	4·2
90–180	17	50	10·4	9	36	9·0	16	29	4·3
180–270	50	90	13·3	36	85	16·0	29	48	6·3
270–360	90	136	15·3	–	–	–	48	80	10·7
360–450	–	–	–	–	–	–	80	133	17·7

and length analyses had shown breaks at this point. However, in each experiment, analyses of covariance revealed no significant differences in the slopes of the data over the two growth phases; therefore only a single equation for the entire life cycle is given for the L–W relationship in each experiment (Table 2).

The slopes of the L–W relationship for LF83 and LF86 were identical (2·59) while LF85 had a higher value (2·80). Analysis of covariance found this higher slope to be significantly different from both LF83 ($P < 0.002$) and LF86 ($P < 0.001$). There was a statistical difference ($P < 0.001$) in the slopes of equations describing the L–W relationship for males and females in LF86 (see Table 7).

Discussion

Laboratory growth data from hatching exist for six species of loliginid squids (Table 8). Growth in these studies (whether measured as weight, mantle length or both) has been found to be exponential in form for at least 2 months post-hatching. Large data sets are available only for *Loligo forbesi* and *Loligo opalescens* Berry that have been reared through most or all of their life cycle. In both species it is clear that growth occurs in two phases: an early rapid exponential phase of 2–3 months followed by a somewhat slower growth phase to sexual maturity. In LF83 and in experiments with *L. opalescens* (Yang *et al.* 1986), this second growth phase was best described by a power function, while in LF86 the second growth phase was best described by a slower exponential function (although a power function provided almost as good a fit to the data). We are inclined to think that the power function is a more realistic growth form for second-phase growth in loliginid squids since various metabolic constraints would seem to preclude true exponential growth in animals growing from sub-adult to adult sizes (see O'Dor & Wells 1987). However, low temperatures might yield metabolic benefits (i.e. lower maintenance costs) which allow slow exponential growth such as that seen in LF86.

An important finding of these culture experiments is that *Loligo forbesi* is clearly capable of sustained exponential growth through and beyond its post-hatching planktonic phase, a period that lasts at least 3–4 months. The observed sustained growth rates for weight ranged from 3·6 to 5·8% BW/d over the first 3 months, while LF88 demonstrated that this species is capable of growth rates of at least 8% BW/d during this part of the life cycle.

The growth rate during this phase of the life history appears to be quite sensitive to temperature. An average temperature difference of only 1°C (13·15 *vs* 14·13°C, respectively) appears to have produced the above-mentioned variation in growth rates and a 3·5°C increase in temperature raised growth rates by approximately 4% BW/d in LF88. Temperature has a significant impact on growth rates, particularly during the early exponential growth phases, and we believe that this effect may explain in part why *L. forbesi* did not attain normal adult size in any of our laboratory culture experiments. In these experiments, we observed a difference in growth rate of about 2% BW/d with a difference in overall mean temperature of only 1°C over the first 3 months (LF85 *vs* LF83). Whether this is the exact magnitude of change in growth rate relative to a 1°C temperature change or not, there is no denying that cephalopod growth rates vary directly with temperature (Forsythe & Van Heukelem 1987; O'Dor & Wells 1987). The temperatures at which *L. forbesi* were grown in our experiments more reflect the ambient sea bottom temperatures at time of egg-laying in nature (i.e.

winter). In reality, with a 2·5–3·0-month egg development, the hatchlings have a chance of encountering spring and early summer surface temperatures in the range of 16–22°C for some part or most of their first 3 months in the plankton.

The impact of a slight rise in growth rate due to warmer temperatures on an animal growing exponentially can be dramatic both in the short-term and long-term. Table 5 illustrates projected wet weights of *L. forbesi* after 90 days of exponential growth at rates of 5–8% BW/d. A hatchling weight of 4 mg is assumed. After 90 days, a hatchling growing at 8% BW/d will be just over 6 times larger than siblings growing at 6% BW/d and this is a realistic growth rate for *L. forbesi* and other loliginid squids. *Loligo opalescens*, a temperate species like *L. forbesi*, grew at 8·4% BW/d for 60 days at a steady 15°C (Table 8 and Yang *et al.* 1986), while the loliginid squid *Sepioteuthis lessoniana* Lesson can grow at 8–13% BW/d for the first 2–3 months at temperatures of 20°C and higher (unpublished results; Segawa 1987). The differences in size at the end of the exponential phase will also have dramatic effects in ultimate adult size. If the four squids grown at the four different rates were all to experience the same overall growth rate of only 1·53% BW/d (that seen in LF86) or 2·0% BW/d (LF83) for the rest of their life span, the remaining projections in Table 5 illustrate their sizes at ages of 12, 15 and 18 months. For comparison, the average size of mature male and female *L. forbesi* from various localities as calculated from published length–weight relationships is given in Table 6.

Table 5 shows that squids exposed to temperatures high enough to produce initial growth at 8% BW/d will be over 10 times larger at one year of age than siblings that grew initially at 5% BW/d. Similar differences are seen at the 15- and 18-month projections. Interpolating from Table 5, squids in excess of 1 kg (1309 g) should be produced by growing *L. forbesi* hatchlings at 8% BW/d for 90 days and then at 2% BW/d (as in LF83) to an age of 365 days. In the laboratory, this scenario would be achieved by growing squids at 17–18°C for 3 months and then 15–16°C for 9 months. Similar interpolations can be made to determine the time needed to attain the squid sizes listed in Table 6. For example, in the Azores, summer surface

Table 5. Estimated growth of *Loligo forbesi* at different growth rates during the first 90 days post-hatching. Further estimates are made using the different 90-day sizes for 9, 12 and 15 months of additional growth at lower overall growth rates of 1·53% and 2·0% body weight per day (%/d)

Hatchling size (g)	Temperature (°C)	Growth rate (%BW/d)	Duration of growth (d)	Estimated size at day 90 (g)
0·004	16–18[a]	8%	90	5·35
0·004	15[a]	7%	90	2·18
0·004	14·5	6%	90	0·88
0·004	14	5%	90	0·36

Starting at 90 day size of	Grown for 275 days @		Grown for 365 days @		Grown for 455 days @ 1·53%/d (14°C)
	1·53%/d (14°C)	or 2·0%/d (16°C)	1·53% (14°C)	or 2·0%/d (16°C)	
5·35 g	359 g	1309 g	1425 g	7919 g[b]	5645 g
2·18 g	146 g	533 g	580 g	3227 g	2300 g
0·88 g	59 g	215 g	234 g	1303 g	928 g
0·36 g	24 g	88 g	95 g	532 g	380 g

[a] Estimated temperature needed to achieve this growth rate.

[b] This is beyond largest known size of *L. forbesi*.

Table 6. The length and weight of mature male and female *Loligo forbesi* from three wild populations. Mantle lengths are published maximum mean lengths of mature animals and wet weights calculated from L–W relationships in Table 6

Locale		Males	Females
Scotland & Faroe Islands	ML (cm)	31	22
Howard (1979)	WW (g)	655	321
South England, Plymouth	ML (cm)	30	25
Holme (1974)	WW (g)	605	394
Central Atlantic, Azores Islands	ML (cm)	57	34
Martins (1982)	WW (g)	2415	910

temperatures reach 22°C (H.R. Martins, personal communication), which would allow growth rates of at least 8% BW/d; subsequent growth after 90 days at only 2% BW/d would yield mature females in less than 12 months and mature males in less than 13 months. The maximum recorded weight for a male in the Azores is 6·2 kg and this would be attained in less than 15 months. The same sort of projections can be made for the English population of *L. forbesi* in Table 6. The authors studying these field populations all predicted approximately 1-year life cycles and these can be realistically predicted from Table 5. The principal assumption required for these projections to be realistic in nature is an abundance of food which would allow for the added energy expenditures of foraging that are not needed in the laboratory.

Sexual dimorphism is a feature of wild populations of *Loligo forbesi* (Table 6) that did not appear in our laboratory populations. Our data suggest that immature males and females are the same size, but as the ovary of females starts to mature they gradually divert more energy from somatic to reproductive growth while males have a minor investment in reproductive tissue and continue to grow somatically (see Forsythe & Van Heukelem 1987). By the time a female spawns, she is much smaller than sibling males of the same age that have continued to grow normally. In our laboratory experiments few animals died of old age, but rather from bacterial infections. Although females were maturing, none reached spawning conditions (Hanlon *et al.* 1989) and it seems that the males may not have lived long enough to out-grow the females as they approached egg-laying.

Slope values obtained for the L–W relationship in these experiments are compared to those reported for *L. forbesi* in nature in Table 7. Our data for males and females fall within the range seen in natural populations; however, the slopes of the equations describing the L–W relation for the whole life cycle are a bit higher. This is certainly due to the inclusion of data for planktonic and juvenile squids, which typically have higher slope values than sub-adults and adults (Forsythe & Van Heukelem 1987).

Table 7. The length–weight relationships for male and female *Loligo forbesi* in laboratory and field populations

	Male	Female
LF83	$W = (1 \cdot 45 \times 10^{-3})$ ML (mm)$^{2 \cdot 22}$; $r^2 = 0 \cdot 9130$	$W = (9 \cdot 88 \times 10^{-4})$ ML (mm)$^{2 \cdot 31}$; $r^2 = 0 \cdot 9270$
LF86	$W = (8 \times 10^{-4})$ ML (mm)$^{2 \cdot 39}$; $r^2 = 0 \cdot 9370$	$W = (7 \cdot 1 \times 10^{-4})$ ML (mm)$^{2 \cdot 94}$; $r^2 = 0 \cdot 9859$
Howard (1979)	$W = 0 \cdot 306$ ML (cm)$^{2 \cdot 2333}$	$W = 0 \cdot 249$ ML (cm)$^{2 \cdot 3161}$
Holme (1974)*	$W = 0 \cdot 229$ ML (cm)$^{2 \cdot 29}$; $r^2 = 0 \cdot 9918$	$W = 0 \cdot 158$ ML (cm)$^{2 \cdot 43}$; $r^2 = 0 \cdot 9925$
Martins (1982)	$W = 0 \cdot 548$ ML (cm)$^{2 \cdot 084}$; $r^2 = 0 \cdot 9933$	$W = 0 \cdot 425$ ML (cm)$^{2 \cdot 184}$; $r^2 = 0 \cdot 9783$

* These equations are modified from original log form by us to match other equations shown.

Table 8. Comparisons of growth phase duration and growth rate for five species of loliginid squids. Experiments with '?' did not approach full life cycle of species

Species	Temperature (°C)	Growth phase duration with mean growth rate as % body weight per day
Loligo forbesi LF83	13–16	⊢—5·8—⊢————————2·0————⊣
Loligo forbesi LF85	12–20	⊢————————3·6————⊣ – – ?
Loligo forbesi LF86	14·0	⊢— 5·1—⊢——————1·53————————⊣
Loligo vulgaris Lamarck Turk *et al.* 1986	17·4	⊢—8·0*——⊢ – – ?
Loligo opalescens Yang *et al.* 1986	15·0	⊢8·4—⊢————2·9———⊣
Loligo pealei Le Sueur Hanlon *et al.* 1987	15–20	⊢——— 5·2*——⊣ – ?
Sepioteuthis sepioidea Blainville LaRoe 1971	20·0	⊢—7·2—⊢——2·8—⊣

```
      0  1  2  3  4  5  6  7  8  9  10  11  12  13  14  15  16
                              Age (months)
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* Weight growth rates estimated from published mantle length growth rates.

Studies of wild squid populations have largely adopted the methodologies used for fish populations, particularly in the areas of fisheries monitoring and management. As more is learned about squid biology, analyses of fisheries data should be modified to take advantage of new information. For instance, the common use of the von Bertalanffy growth function to model squid growth is quite questionable (Lange 1980; Macy 1980; Forsythe & Van Heukelem 1987; Saville 1987) since cephalopods clearly do not grow asymptotically. Other growth models should be used based upon available information. Another example is the importance of temperature on the potential productivity of a fisheries resource. Temperature is not so important in the study of fish populations since slight changes in temperature do not significantly affect fish growth and it is not taken into account in modelling. Nearly the opposite is true of cephalopods where, except for food abundance, possibly nothing has a stronger influence on growth than temperature. We have already shown in this paper and one other (Forsythe & Hanlon 1988), at least hypothetically, how growth at different temperatures could result in cephalopods of dramatically different size and life span. It is hoped that laboratory studies can contribute to increasing the accuracy of fisheries modelling techniques in coming years.

Acknowledgments

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