

Abstract.—The effect of maturation on relative growth of somatic tissues was investigated by measuring and comparing monthly changes in dry weight of somatic tissues and reproductive organs. In both sexes, reproductive tissues grew in relation to total body mass; at maturity female reproductive tissue was 16% of total dry body mass, whereas male reproductive tissue was 2.6%. In females, the relative mass of the mantle and head decreased during maturation, whereas the relative mass of the viscera increased. In males, the mass of the viscera increased with maturation, but no decreases occurred. The percentage composition of protein in the mantle and head of females for each maturity stage did not differ significantly. For both sexes, the digestive gland mass remained relatively constant throughout the different maturity stages and seasons, and analysis of stomach fullness indicated that feeding increased in the final maturity stages. All observations support the hypothesis that energy and nutrients for maturation are supplied mainly by diet rather than by stored resources, but that during maturation there is a shift of emphasis from somatic growth to gonadal development and vitellogenesis. *Sepia pharaonis*, which appears to be an intermittent multiple spawner, does not use protein from muscle tissue for developing and growing its reproduction tissues.

Reproductive versus somatic tissue growth during the life cycle of the cuttlefish *Sepia pharaonis* Ehrenberg, 1831

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Cephalopod mollusks have various life history strategies, ranging from typically semelparous (e.g. many coleoids) to iteroparous (e.g. *Nautilus* spp.) (Boyle, 1983, 1987). Different modes of semelparity may occur, and this diversity may be related in part to growth patterns (Mangold et al., 1993). Most cephalopods that have been studied are fast growing, and they generally reproduce once and die (Calow, 1987). However, others have intermittent growth (Boletzky, 1987; Forsythe and Van Heukelem, 1987; Jackson and Choat, 1992) and multiple spawning events (Harman et al., 1989; Lewis and Choat, 1993). We investigated the relation between reproduction and somatic growth in the commercially valuable cuttlefish *Sepia pharaonis* Ehrenberg, 1831.

For many marine invertebrates, reproduction represents an enormous energy investment, and achieving the optimum balance between somatic and reproductive effort is critical to an individual's lifetime fitness (Calow, 1981). The variations in reproductive strategies usually correlate with variations in

feeding and growth patterns. Assessing the cost of reproduction is difficult, and although slowing of somatic growth may indicate the allocation of energy to oocyte production, an assessment of somatic tissue may provide a better indicator of the cost of reproduction (Calow, 1983).

For example, in some benthic octopuses, mantle protein is mobilized to provide energy for egg development; the subsequent depletion of protein from body tissues probably contributes to the death of some octopus females (Tait, 1986; Pollero and Iribarne, 1988). This would not seem to be a sensible strategy for a swimming cephalopod, such as cuttlefish, which still requires functional muscle to survive in the water column. *Sepia pharaonis*, which migrates to spawning grounds from its feeding grounds (Gabr et al., 1998), would certainly need to maintain swimming ability.

Elucidation of patterns of energy storage and utilization is important in understanding the interaction between organism and environment (Clarke et al., 1994). Although many studies indicate that oocyte produc-

tion affects the growth and condition of somatic tissue in squid (e.g. Rowe and Mangold-Wirz, 1975; Hatfield et al., 1992), few studies have examined the expenditure of nutrients and energy for the development of reproductive organs in cuttlefish. Boucaud-Camou (1971) found that the digestive gland of *Sepia officinalis* has high concentrations of lipids, suggesting that it acts as a storage organ. Castro et al. (1991) studied changes in the digestive gland of *S. officinalis* and *S. elegans* throughout their life cycles and observed that the digestive gland weight of *S. officinalis* decreased progressively with starvation. However, there is no evidence that the digestive gland provides stored energy for gonad development.

Sepia pharaonis is widely distributed in the Indo-Pacific from the Red Sea to Japan and Australia. Together with *S. dollfusii*, it is the primary fishery in the Suez Canal and the most valuable commercial cephalopod in the northern Indian Ocean (Nesis, 1987). Little is known about the biology of this species (Silas et al., 1985; Aoyama and Nguyen, 1989; Gabr et al., 1998). In this paper, we examine aspects of its life history to determine if a trade-off exists between somatic and reproductive tissues. We measured food intake to determine whether nutritional activity was involved in the development of reproductive organs.

Materials and methods

Samples of *Sepia pharaonis* were collected monthly from Bitter Lake, the main fishing port in the Suez Canal, from September 1994 to April 1996. In total, 1428 females and 1151 males were examined. The dorsal mantle lengths ranged from 10 to 240 mm. Specimens were dissected to determine sex and maturity stage. Four maturity stages for each sex were determined by using a modification of the scale proposed by Mangold-Wirz (1963) and refined in detail for *Sepia pharaonis* by Gabr et al. (1998): for females, I=immature, II=maturing, III=pre-spawning, and IV=spawning; for males, I=immature, II=maturing, III=fully mature, and IV=spawning.

Dorsal mantle length (ML) and nidamental gland length (NGL) of females were measured to the nearest mm. The following measurements of mass were made to two decimal places (in grams): total body mass (BM); total somatic mass (SM); mantle mass (MM); head mass including arms and tentacles (HM); digestive gland mass (DGM); viscera mass (VM) including gills, stomach, caecum, pancreas, ink sac; ovary mass (OM) including oviduct; testis mass (TM); nidamental gland mass (NGM); and spermatophoric complex mass (SCM).

Relative assessment of somatic tissue growth

Two statistical analyses were conducted to determine if somatic tissue declined in relation to size during maturation. All statistical analyses were carried out by using the MINITAB statistical package and all data were \log_{10} -transformed.

In the first analysis, a multiple regression was applied to the female data only by using \log_{10} mantle length and \log_{10} nidamental gland length as independent variables. These variables were selected because they correlated with our maturity scale (Gabr et al., 1998). Multiple regression equations were obtained for log-transformed total somatic mass and for masses of mantle, head, digestive gland, viscera, and ovary (including oviduct and oviductal gland, and nidamental gland). This analysis allowed for the use of a continuous variable in the assessment of maturity over the whole size range of the sampled population. This multiple regression analysis was carried out only on females because length was used in the analysis. To carry out a similar exercise with male cuttlefish, the relation of the log-transformed mass of each organ with spermatophoric complex mass (SCM) and body mass would have to be used. These variables would lead to problems in scaling because they would involve autocorrelation, which would distort perceived relationships (LaBarbera, 1989). The ratio of SCM to ML has not been tested before as an objective measure of maturity in male cuttlefish and therefore no analysis was included here.

In the second analysis, a multivariate analysis of covariance (ANCOVA) was applied to the total somatic mass, individual somatic organs, and reproductive organs, whose relationships with the reproductive cycle were considered dependent variables (Garcia-Berthou and Moreno-Amich, 1993). Mantle length was treated as the covariate. A fundamental assumption of standard ANCOVA (McCullagh and Nelder, 1983) is the homogeneity of regression coefficients (slopes) of dependent variable and covariate relationships. This assumption can be tested with a special design of ANCOVA, by analyzing the pooled covariate by factor interaction. If the covariate by factor interaction is significant, standard ANCOVA should not be developed. Otherwise, if the covariate by factor interaction is not significant, the standard ANCOVA design is the preferred method. For the cases with significant effect with factor (maturity stage), the variation can be described by using the predicted means for each cell, adjusted for the effect of the covariate. We set the alpha level for statistical significance at 0.001 to identify the strongest effects of maturity on the dependent variables.

Dry weight analysis

To study the seasonal variation in somatic and reproductive organs, dry weight was used to correct for differences in water content between different organs. The samples for this study were collected from November 1994 to April 1996. From each monthly sample, a subsample of 20 females and 20 males was selected with mantle lengths within a 20-mm size range encompassing the mean size at maturity (the size at which 50% of the individuals were maturing or mature). This size was 122 and 61 mm ML (calculated by using the whole-year sample) for females and males, respectively (Gabr et al., 1998). It is possible to treat specimens from around the mean as "standard" animals (*sensu* Gabbott, 1976) and so compare cuttlefish at different degrees of maturity without having to make statistical corrections for size. There were no cuttlefish of maturity stage I in this subsample; however, stages II to IV were present. The cuttlefish in the subsample were dissected in the same way as those in the sample as a whole. The same measurements of mass to two decimal places (in grams) were taken, but dry rather than wet weight was used. Tissues were dried to constant weight (for 48 h) at 80°C and then cooled in a desiccator.

The following indices were calculated for dry weight tissues: gonadosomatic index for females (GSI) = 100 OM/BM; gonadosomatic index for males (GSI) = 100 TM/BM; nidamental gland index (NGI) = 100 NGM/BM; spermatophoric complex index (SCI) = 100 SCM/BM; mantle index (MI) = 100 MM/BM; head index (HI) = 100 HM/BM; digestive gland index (DGI) = 100 DGM / BM, and viscera index (VI) = 100 VM/BM.

Analysis of protein

The dry tissue of mantle and whole head for 7 to 9 females of maturity stages II–IV was ground to a fine powder with a mortar and pestle. The powdered samples were placed in sealed plastic vials and stored for further analysis. The Kjeldahl method for determination of nitrogen was used (see Giese, 1967). % Protein = % nitrogen \times 6.25 (Giese, 1967; Rigby, 1990; Dickey-Collas, 1991). Kruskal-Wallis ANOVA was used to examine the significant variation in percentage of protein between maturity stages.

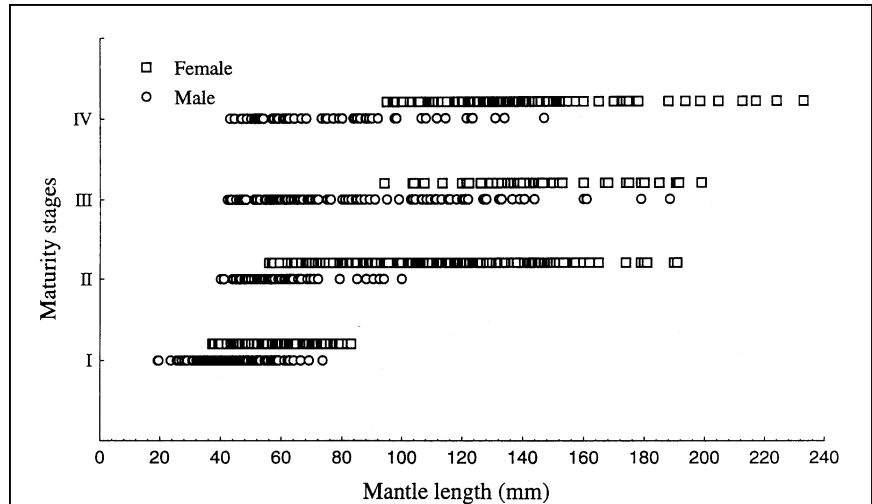


Figure 1

Relation between mantle length and maturity stages in female and male *Sepia pharaonis*.

Stomach content analysis

Each specimen's stomach fullness was estimated according to a 5-level subjective scale: 0=empty; 1=one-quarter full; 2=half full; 3=three-quarters full; 4=full or distended.

Length-weight relationship

Equations of the form $BW = aML^b$, where a and b are constants of the regression, were fitted by transforming the data into \log_{10} and deriving the regression line by the least squares method. Correlation was expressed by the coefficient r^2 , and comparisons between males and females were made by ANCOVA.

Results

Growth and maturity

Maturity generally increased with mantle length, but each stage was represented by a very wide range of mantle lengths with considerable overlap between stages (Fig. 1). This finding suggests that there is no strong relation between growth and maturation rate. Males attained full maturity (stage III) at a smaller size than females (stages III and IV).

Maturity stages versus soma production and gonad production

In females (Table 1), there was a significant increase in total somatic mass and mass of somatic organs

Table 1

Intercepts (a) and slopes (b_1 and b_2) \pm SD for multiple regression equations relating mantle length (b_1) and nidamental gland length (b_2) to tissue masses for female *Sepia pharaonis*. The equation is $\log \text{tissue mass} = a + b_1 \log ML + b_2 \log NGL$. P is level of significance (* indicates significant relationships i.e. $P < 0.05$); s is residual standard deviation about the regression lines; r^2 is adjusted proportion of variation accounted by the variance model; and n is number of specimens.

	a	b_1	P	b_2	P	s	r^2	n
Independent variables: mantle length; nidamental gland length								
Dependent variables: 0.0001*								
Total somatic mass	-0.87 \pm 0.05	2.92 \pm 0.04	0.0001*	-0.09 \pm 0.02	0.0001*	0.24	0.99	191
Mantle mass	-1.22 \pm 0.05	2.98 \pm 0.05	0.0001*	-0.14 \pm 0.02	0.0001*	0.59	0.98	226
Head mass	-1.21 \pm 0.04	2.84 \pm 0.04	0.0001*	-0.08 \pm 0.02	0.005*	0.25	0.99	191
Digestive gland mass	-2.20 \pm 0.10	2.98 \pm 0.11	0.0001*	-0.02 \pm 0.05	0.690	1.78	0.93	192
Viscera mass	-1.71 \pm 0.03	2.58 \pm 0.13	0.0001*	0.03 \pm 0.06	0.580	2.4	0.89	192
Ovary mass	0.49 \pm 0.36	-1.66 \pm 0.41	0.001*	3.50 \pm 0.16	0.0001*	17.33	0.93	176
Nidamental gland mass	-0.17 \pm 0.26	-0.65 \pm 0.29	0.030	2.92 \pm 0.11	0.0001*	9	0.96	176

(i.e. mantle, head digestive gland and viscera masses) with mantle length ($P < 0.05$). The effect of ML on reproductive organ mass (i.e. ovary, nidamental gland masses) also was significant ($P < 0.05$). In relation to nidamental gland length, there was a small but significant decrease ($P < 0.05$) in total somatic mass, mantle mass, and head mass, whereas the relative decrease in digestive gland mass and viscera mass was not significant ($P > 0.05$). As expected, there was also a highly significant increase ($P < 0.05$) in reproductive organ mass with maturity (NGL).

The second analysis was an analysis of multivariate covariance (ANCOVA). In an animal that matures at a wide range of body sizes, it is difficult to quantify the pattern of maturation because comparisons of individuals of different sizes cannot be thought of as indicating the pattern of growth and maturation of any one animal. Thus, although some animals matured at 60 mm ML, others remained immature at larger sizes (Fig. 1). ANCOVA corrects for the variation in size (ML) of animals within maturity stages.

Table 2 shows the initial standard ANCOVA design to test for homogeneity of slopes. In females, there was significant effect of an interaction between the factors (maturity stage) and covariate (mantle length) for OM and NGM. The effect of interaction of mantle length and maturity stages on TSM, MM, HM, DGM, and VM was not significant ($P > 0.001$). Thus in these cases the hypothesis of homogeneity of slopes was accepted; therefore further analyses were required to test the effect of maturity stages for these variables. In males, there was a highly significant effect ($P < 0.001$) between mantle length and maturity stage for all log-transformed dependent variables except spermatophoric complex mass. Thus for these variables the hypothesis of homogeneity of

slopes was rejected and further analysis was not possible (i.e. the standard ANCOVA design should not be developed for these cases).

The results of the final ANCOVA design (in the cases where the effect of mantle length and maturity stage interactions were not significant) are indicated in Table 3. In female *Sepia pharaonis*, maturity significantly affected TSM, MM, HM, and VM ($P < 0.001$) but did not significantly affect DGM ($P > 0.001$). In males, maturity significantly influenced spermatophoric complex mass ($P < 0.001$).

Figure 2 shows the adjusted means for each dependent variable for each maturity stage after the removal of the mantle length (covariate) effect when the effects of maturity stages were found to be significant. For females, there was a decrease in total somatic mass, mantle mass, and head mass with increasing maturity stage. There was a decrease in viscera mass from stage I to stage III followed by an increase at stage IV (Fig. 2A). For males, there was an increase in relative mass of spermatophoric complex mass with increasing maturity stage (Fig. 2B).

Monthly variation in soma versus gonad production

Monthly fluctuations in mean dry weight indices for individual organs of somatic tissue (mantle index, MI; head index, HI; digestive index, DGI; and viscera index, VI) and reproductive tissue (gonadosomatic index, GSI; nidamental gland index, NGI; and spermatophoric complex index, SCI) for females and males are illustrated in Figures 3 and 4, respectively. These indices displayed monthly fluctuations and indicated the relative proportion that each body component contributed to the weight of the entire body. The mantle mass was always the largest component

Table 2

Preliminary design of ANCOVA for *Sepia pharaonis*. In each case, mantle length is the covariate, maturity stage (I–IV) is the factor, and the dependent variables are total somatic mass (TSM), mantle mass (MM), head mass (HM), digestive gland mass (DGM), viscera mass (VM), ovary mass (OM), nidamental gland mass (NGM), testis mass (TM), and spermatophoric complex mass (SCM). The homogeneity of slopes was tested with a pooled covariate by factor interaction: *F*-statistic. Significance levels ($P < 0.001$) are indicated by an asterisk.

	Mantle length (ML)		Maturity stages (MSt)		ML × MSt	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Female						
TSM	11000.00	<0.001*	2.80	0.039	1.87	0.130
MM	11000.00	<0.001*	4.74	0.003	2.81	0.030
HM	10000.00	<0.001*	5.29	0.001	3.93	0.009
DGM	3440.00	<0.001*	2.18	0.089	2.16	0.092
VM	2926.30	<0.001*	0.40	0.754	0.98	0.400
OM	271.07	<0.001*	25.15	<0.001*	29.87	<0.001*
NGM	513.73	<0.001*	166.10	<0.001*	317.58	<0.001*
Male						
TSM	918.60	<0.001*	22.00	<0.001*	23.00	<0.001*
MM	1745.94	<0.001*	14.32	<0.001*	13.66	<0.001*
HM	1295.97	<0.001*	12.50	<0.001*	11.02	<0.001*
DGM	849.18	<0.001*	11.15	<0.001*	9.55	<0.001*
VM	853.13	<0.001*	5.96	<0.001*	5.28	<0.001*
TM	612.65	<0.001*	294.18	<0.001*	15.52	<0.001*
SCM	749.19	<0.001*	6.01	<0.001*	0.88	0.450

proportionally, followed by the head mass. Thus, *S. pharaonis* weight gain and loss were accounted for mainly by the mantle and head mass that underwent fluctuation in mean dry weight index during the study.

The MI and HI diminished considerably as gonad development proceeded. The largest decrease in MI and HI of females occurred in spring and summer (from March to September), as shown in Figure 3. These indices decreased from 52% to 41% and from 34% to 28%, respectively. In contrast, during the same period the gonads (GSI, NGI) exhibited development; GSI increased from 1% to 9% and NGI increased from 2% to 7%. VI increased rapidly from May to November, from 5% to 10%. DGI showed little change over the whole sampling period (ranging between 7% and 10%).

By contrast, in male *Sepia pharaonis*, the MI, HI, and DGI remained relatively constant throughout the entire sampling period (Fig. 4). The pattern of VI was consistent with the situation in female, increasing from 5% to 8% during the period from May to October. There was a gradual increase in GSI and SCI from November, reaching the highest value in May ($\approx 1.3\%$), and spawning after June was indicated by a decline in GSI and SCI.

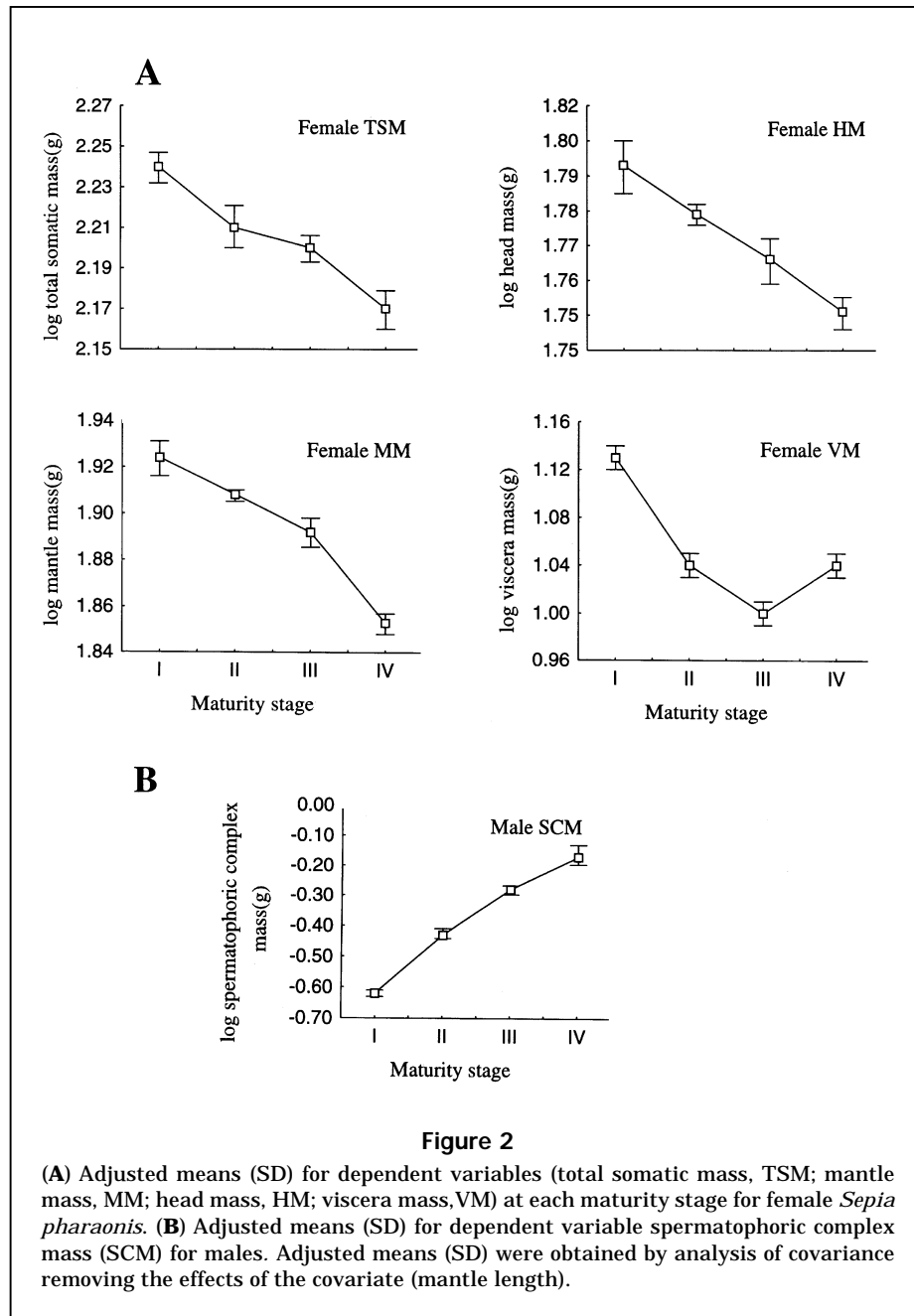
Table 3

Final design of ANCOVA for *Sepia pharaonis* data for which the homogeneity hypothesis was accepted, *F*-statistics, and *P*-values. See Table 2 for definitions of abbreviations. Significance levels ($P < 0.001$) are indicated by an asterisk.

	Mantle length (ML)		Maturity stages (MSt)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Female				
TSM	15000.00	<0.001*	25.130	<0.001*
MM	16000.00	<0.001*	40.570	<0.001*
HM	14000.00	<0.001*	10.470	<0.001*
DGM	4770.00	<0.001*	0.680	0.560
VM	4031.89	<0.001*	11.270	<0.001*
Male				
SCM	901.800	<0.001*	133.890	<0.001*

Percentage of protein, water content, and maturity stage

The mean percentage composition of protein and mean percentage of water content in the mantle and head of females for maturity stages II–IV is shown



in Table 4. In neither mantle nor head was there significant variation ($P > 0.05$) in percentage of protein or water content with maturity stage.

Stomach fullness in relation to maturity stages

The stomach fullness for each maturity stage for each sex is illustrated in Figure 5. The degree of stomach fullness remained relatively constant through the maturity stages, indicating that *Sepia pharaonis* continued to feed when mature.

Length-weight relationship

The length-weight relationship for *Sepia pharaonis* is described by the equation: $Wt = 0.27L^{2.65}$, $r^2 = 0.99$, $n = 966$ for females, and $Wt = 0.28L^{2.60}$, $r^2 = 0.99$, $n = 723$ for males. The elevation and slopes from the regression equations for females and males did not differ significantly, thus indicating that females have approximately the same weight as males at the same mantle length, and that both sexes increase similarly in weight per unit gain in mantle length.

Discussion

This study describes the pattern of allocation of resources to the growth of somatic and reproductive tissues in *Sepia pharaonis*, one of the two most commercially important cephalopods in the Suez Canal and northern Indian Ocean. This study indicates that gametogenesis is fueled by energy and nutrients derived from the diet rather than from reallocation of somatic reserves. Two complementary methods (analysis of covariance and multivariate regression on the entire data set) and the monthly changes in

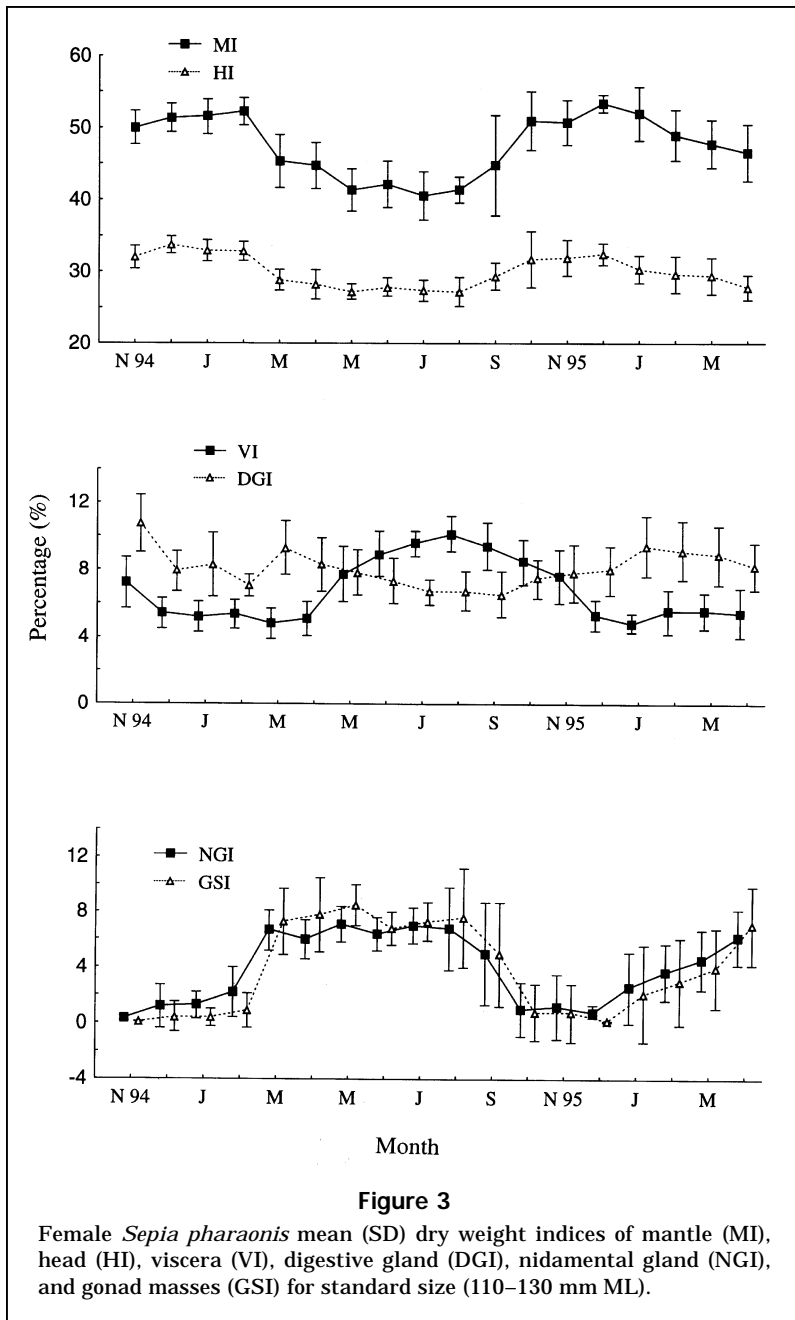
dry weight of somatic indices of a restricted size range showed essentially similar patterns of maturation.

Sexual maturation in *Sepia pharaonis* affected males and females differently. Forsythe and Van Heukelem (1987) suggested that male maturity in cephalopods was achieved at little cost to somatic growth and that, in most cases, males continue to grow after reaching maturity. Changes in male somatic mass do not appear to be related to maturity. At full maturity in males, dry weight of reproductive and accessory reproductive tissues accounted for only 2.6% of the total somatic dry weight. However,

these tissues accounted for approximately 16% in females. For both sexes, somatic growth was completed by late October as the average mantle mass and head mass components reached maximum weights.

In females, spawning occurred from spring throughout the summer, and the end of spawning activity was reflected by a sharp drop in the average gonad weight index in October (Fig. 3). Thus spawning occurred at the time of increasing temperature and food availability (Gabr, unpubl. data). There was no evidence of decline in feeding rate with maturation. This finding suggests that gonadal growth may be supported directly by the assimilated food ration, although some diversion of resources into reproduction at the expense of somatic growth also occurred. This diversion of resources was indicated by a small but significant decrease in mantle and head mass with maturation (Fig. 2), and the inverse relationship of mantle and head mass with gonadal indices (Fig. 3).

There is some evidence to support the idea that female *Sepia pharaonis* may feed, grow, and mature simultaneously in the field. For example, no spent females were caught at any time of the year. This may be because it is difficult to differentiate spent females from mature ones if spent females remain in good condition (because they continue to feed when mature). Because females need a greater energetic reserve for reproduction, they grow faster than males and reach a maximum size of 240 mm ML, whereas the maximum size for males was 170 mm ML. *Sepia pharaonis* spawns in shallow water and migrates

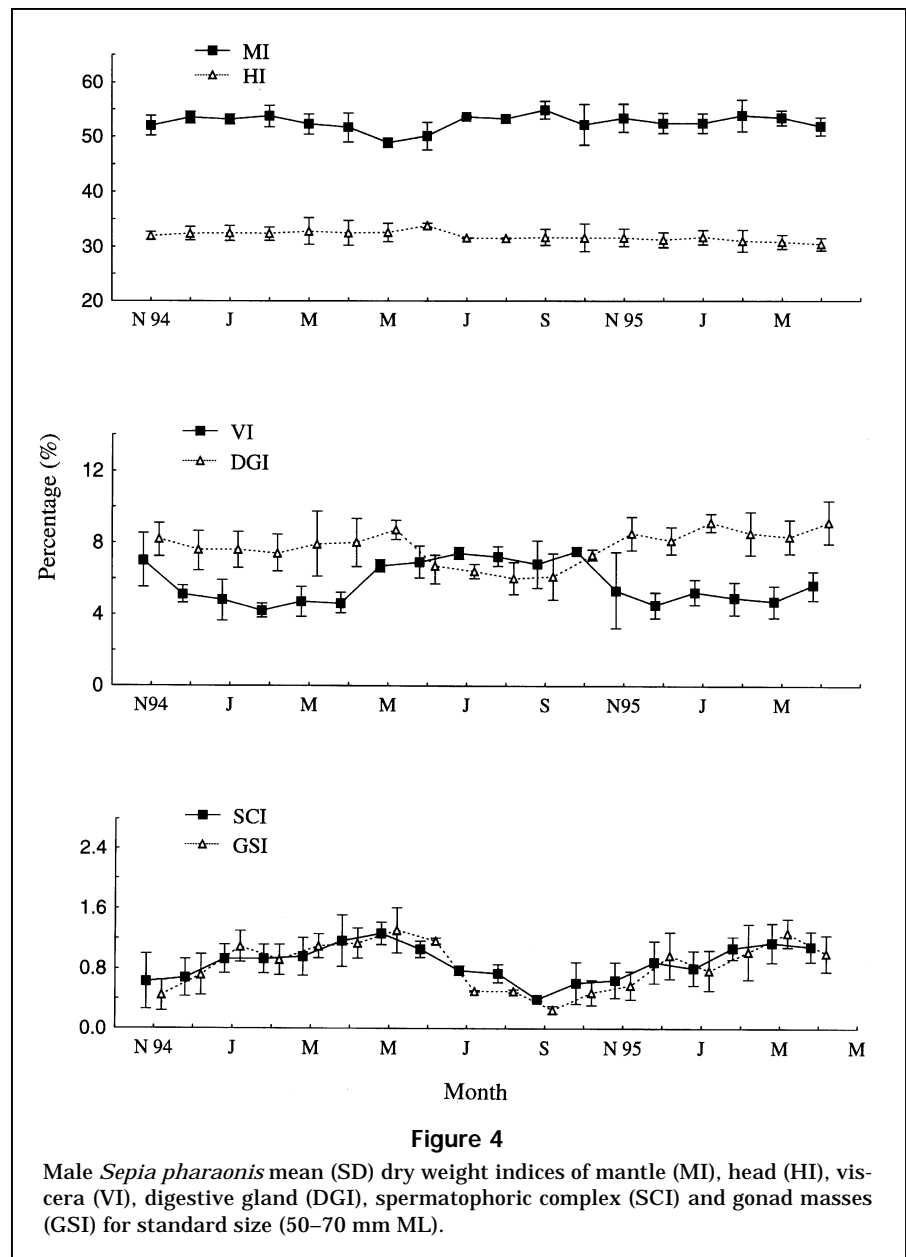


offshore after spawning either to die or to return to spawn again; such a migration is unlikely to be preceded by any degradation of mantle muscle, which is the major organ for locomotion in cuttlefish. In neither mantle nor head was there a significant variation in percentage of protein or water content with maturity stage. These data indicate that female *S. pharaonis* possibly do not use mantle or head tissue to fuel gonadal development, at least during the beginning of the spawning season.

In sharp contrast, studies of another cuttlefish, *Sepia dollfusii* (Gabr et al., in press), have demonstrated that this species seems to use mantle muscle as an energy source during gonadal development. There thus appears to be a continuum in cuttlefish reproductive strategy. At one end, spawning is associated with gonad maturation at the expense of somatic tissue. At the other end, growth of reproductive organs takes place through the use of energy and nutrients derived from the diet, not through mobilization of nutrients and energy from somatic tissue.

The results of this paper agree with some studies on the squid *Illex argentinus* (Hatfield et al., 1992; Rodhouse and Hatfield, 1992; Clarke et al., 1994). Although mantle mass of female *Illex argentinus* decreases in relation to ML with maturity, this is not associated with degradation or changes in the biochemical composition of mantle muscle. Studies on *Loligo forbesi* (Collins et al., 1995), *L. gahi* (Guerra and Castro, 1994) and *Photololigo* sp. (Moltschaniwskyj, 1995) have also demonstrated that maturation and growth occur simultaneously during most of the life cycle and that the condition of the squid remains high at maturation.

The digestive gland showed no loss of mass during maturation. Boucaud-Camou (1971) indicated that the digestive gland of *Sepia officinalis* could act as a lipid storage organ, and Blanchier and Boucaud-



Camou (1984) found that the variation in lipid levels of the digestive gland seemed more related to diet than to sex or maturity state of the gonads. There was no significant variation in the digestive gland weight with maturity state and season. Thus, the digestive gland mass cannot be used as an indicator of feeding activity in *S. pharaonis* as it can in some squid (Abolmasova et al., 1990) because no increase in DGI was found in the season of high feeding activity. This agrees with Castro et al. (1991), who found no significant variation in the digestive gland weight with season in *S. officinalis* and *S. elegans*.

In conclusion, this study shows that the pattern of intermittent spawning suggested by our previous

Table 4

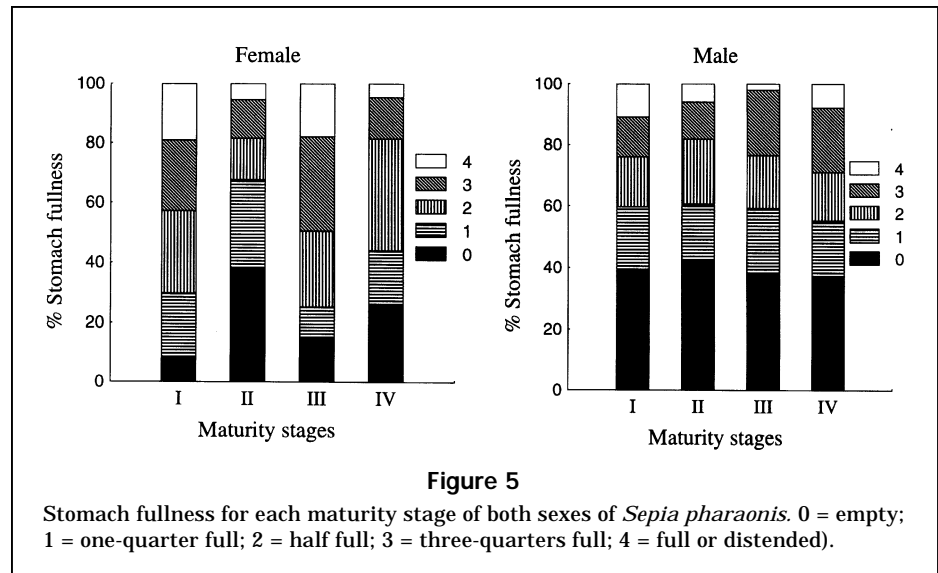
Summary of mean \pm SD values of percentage of protein and water content in mantle and head dry tissue with maturity stages for female *Sepia pharaonis*.

Maturity stage	Number	% Protein		Number	% Water content	
		Mantle	Head		Mantle	Head
II	9	78.33 \pm 0.68	76.21 \pm 0.32	66	75.83 \pm 1.4	79.38 \pm 1.4
III	8	79.78 \pm 0.41	76.23 \pm 0.39	20	76.18 \pm 1.3	79.64 \pm 1.06
IV	7	78.19 \pm 0.39	75.82 \pm 0.53	79	75.48 \pm 1.8	78.91 \pm 1.5
Kruskal-Wallis ANOVA:	<i>H</i>	2.08	0.24		1.32	3.37
	<i>P</i>	0.35	0.88		0.51	0.18

study of this species (Gabr, et al., 1998) is quite likely, partly because the spawning season is greatly protracted (Fig. 3). Indeed, it appears that this species is capable of meeting the demands of oocyte production without metabolizing reserves of other tissues. Both males and females continue to feed as maturity is reached, thus energy for gonad production is diverted primarily from the food supply, although some diversion from somatic tissue may also occur. In the context of this paper and results from *S. dollfusi* (Gabr et al., in press), variation in reproductive strategies correlates with variations in feeding and growth patterns as suggested previously for other coleoids (Mangold et al., 1993).

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