Life cycle, demography and reproductive investment in the myopsid squid *Alloteuthis subulata*

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ABSTRACT: Eleven monthly samples of the myopsid squid *Alloteuthis subulata* were collected from the English Channel with a small otter trawl in 1985–86. Squid were sexed and assigned a maturity stage. Measurements were made of mantle length and dry weight of gonad and somatic tissue. Maximum length of life for squid from this population is ca 1 yr. Immature squid are recruited into the population twice during the year, in spring and summer. Males and females start to mature at 30 to 40 mm mantle length. The demography of the population is complex, and more difficult to interpret for males. There were apparently 3 spawning groups of females in the year sampled. The length exponent for body weight is very low in both males and females. Males mature earlier than females and male gonad weight is poorly correlated with body weight in squid > 90 mm mantle length. Gonad weight increases logarithmically in relation to total body weight in females but gonad production is not appreciable until mantle length exceeds 100 mm. The gonad accounts for ca 25 % of the body mass of females at the maximum mantle length of 140 mm. This suggests that *A. subulata*, in common with some other cephalopods, has a low reproductive effort by comparison with the lifetime reproductive effort of species of benthic iteroparous mollusc.

INTRODUCTION

Current life-history theory, as reviewed by Stearns (1976, 1977) and Sibly & Calow (1983), predicts how organisms may divide resources between somatic growth and gamete production to maximize Darwinian fitness. In all organisms the allocation of resources to reproduction, or reproductive effort, is expected to bear an inverse relation to residual reproductive value or the expectation of future production of offspring (Williams 1966, Hirshfield & Tinkle 1975, Pianka 1976). Theory predicts that semelparous species will have a higher reproductive effort than iteroparous species and that in the latter, reproductive effort will increase with age.

These predictions have been tested in a number of iteroparous and semelparous species of bivalve and gastropod mollusc (Fuji & Hashizume 1974, Browne & Russel-Hunter 1978, Rodhouse 1978, Richardson 1979, Thompson 1979, Hughes & Roberts 1980, Vahl 1981, Bayne et al. 1983, Rodhouse et al. 1984, Barber & Blake 1986). Reproductive effort does generally increase with age in iteroparous species, but whilst some authors

(Browne & Russel-Hunter 1978, Barber & Blake 1986) found that reproductive effort was greater in semelparous species, others (Hughes & Roberts 1980) found less difference.

The extant coeloid cephalopods are, almost without exception (Rodaniche 1984), semelparous and so provide valuable material for the study of evolution of molluscan life-history patterns. However, they have received little attention in this respect. In a recent review Calow (1987) concluded that, with only 2 exceptions, reproductive effort of the semelparous cephalopods is low in comparison with iteroparous bivalves and gastropods.

When making these comparisons, Calow (1987) used the ratio of biomass invested in eggs to parental biomass as an index of reproductive effort. This index differs from the more comprehensive definition of reproductive effort, which is a measure of the proportion of the organism's energy budget which is allocated to gonad and the metabolic cost of gonad synthesis and reproductive activity (see Clarke 1987 for a recent review). In view of the practical difficulties of collecting

data on all components of the energy budget of squid, reproductive investment in this study is measured as the proportion of total net tissue production allocated to gonad: $P_r/(P_r + P_g)$, where P_r is production of gametes and P_g is production of somatic tissue. This ratio, elsewhere termed reproductive effort (Browne & Russell-Hunter 1978), excludes the metabolic cost of gamete production and ignores turnover in gonad and somatic tissue. However, it has the merit of allowing a comparison of reproductive investment in semel- and iteroparous molluscs because the sum of lifetime gonad production, in iteroparous species, can be expressed as a proportion of lifetime total net tissue production to give a measure of lifetime reproductive investment.

There is a clear need for more precise, quantitative data on the growth and reproduction of individual species of cephalopod. The myopsid squid *Alloteuthis subulata* (Lamarck) can be caught in the western English channel throughout the year by trawling and so is a suitable subject for life cycle analysis. It occurs from the North Sea and western Baltic south to the Sahara banks and throughout the Mediterranean (Roper et al. 1984). In the English Channel it is close to the centre of its latitudinal range.

MATERIALS AND METHODS

Monthly samples of *Alloteuthis subulata* were collected from the English Channel, in the vicinity of Whitsand Bay, Cornwall, UK, between March 1985 and January 1986. Samples were taken using a small otter trawl, with a 15 m ground rope. The wings of the trawl were of 32 mm mesh and the belly, cod-end and baiting were of 25 mm mesh. A sleeve of 13 mm mesh surrounded the cod-end for a distance of 1 m on the belly and 4 m on the back. A plastic tub fitted in the cod-end reduced damage to the squid after capture. Hauls were made between 08:00 and 12:30 h at depths of 8 to 60 m.

The dorsal mantle length of every specimen from each monthly sample was measured to the nearest mm with vernier calipers. Each squid was assigned a maturity stage on a scale 0 to VI, after Holme (1974). This scale is a subjective measure of sexual maturity based on the appearance of the reproductive system as well as the size of the gonad. In this respect the appearance of the secondary sexual organs – nidamental glands in females and Needham's sac in males – is predominant in assessing maturity. From each sample ca 25 males and 25 females were then selected to represent the size range for the analysis of relative growth. The gonad was dissected from the soma and both tissues dried to constant weight (24 h) at 80° C. After drying, the tissues were cooled in a desiccator and weighed to 0.1 mg.

Size frequency distributions of monthly catch data for immature, male and female squid, as identified by morphological features, were plotted and analysed by the method of MacDonald & Pitcher (1979), using the interactive software package 'MIX' (MacDonald & Green 1985). Inspection of the data revealed that size classes in the distributions were easily recognizable, especially in the data for immatures and females, and that there were never more than 2 size classes present. This is consistent with the observation that *Alloteuthis subulata* lives for 1 to 2 yr (Roper et al. 1984). The 'MIX' programme was used to obtain objective estimates of the mean size, and standard deviation, for each size class identified by inspection. With 1 exception, parameter estimates were obtained in all cases within 20 iterations; for the July sample of males it was necessary to constrain the proportions of the 2 size classes present. The data were therefore considered to meet the criteria necessary for the application of the 'MIX' programme (Grant et al. 1987).

All other statistical procedures were performed using the 'GENSTAT 5' statistical package (Payne et al. 1987).

Relative growth of gonad and soma. Allometric equations relating total body weight to mantle length, and gonad weight to total body weight (Table 1), were used to calculate the relative growth of soma and gonad in males and females.

Table 1. *Alloteuthis subulata*. Regression equations relating total dry body weight (TDBW) to mantle length (ML) and gonad weight (GW) to TDBW

Independent variable	Dependent variable	Sex	Months	Intercept (±SE)	Slope (±SE)	$\overline{R}^2$
$\log_{10}ML$	$\log_{10}TDBW$	M	All	−2.39 (± 0.050)	1 31 (± 0.027)	0.89
		F	All	−3.03 (± 0.079)	1.70 (± 0.043)	0.87
$\log_{10}ML$	$\log_{10}GW$	M	Oct–Dec	−2.04 (± 0.026)	1.17 (± 0.107)	
			Jan–Sep	− 1.72 (± 0.031)	1.17 (± 0.107)	0.56
		F	Nov–Jan	−2.17 (± 0.040)	1.73 (± 0.270)	
			Mar–Oct	−1.69 (± 0.052)	2.75 (± 0.298)	0.78

RESULTS

Catch per unit effort

Catch per unit effort (CPUE) is expressed here as numbers of squid caught per hour (Fig. 1). There were 2 peaks of CPUE for immature squid; these were in May and November. Both these peaks followed a decline, and preceded an increase, in the CPUE for adults. This suggests that recruitment of immature squid followed spawning and subsequent mortality of adults, and that recruitment of adults closely followed recruitment of immatures.

Length-frequency structure

Monthly length-frequency distributions for immatures, females and males are illustrated in Fig. 2.

Immatures. Immature squid of indeterminate sex occurred up to a mantle length of 50 to 60 mm although there was discernible sexual development in some squid smaller than this. Small numbers of immatures were present in the population throughout the year. There was a minor period of recruitment in May and a major, extended, period of recruitment during October, November and December. The mean mantle length of immatures increased from 38 to 48 mm during this period.

Males. Males were recognizable at a mantle length of 30 to 40 mm. At the start of the sampling programme in March the population contained 2 size classes, representing cohorts born in 1984, with means at 65 and 114 mm. These grew so that in May the means were at 70 and 143 mm. There was apparently some recruitment of males in June, which gave rise to a cohort with a mean size of 58 mm. During July, August and Sep-

tember there was little change in the male population size frequency structure apart from an increase in the mean of the small size class to 67 mm in September. In October large squid, > 90 mm, had disappeared from the population. In November a second 1985 cohort, with a mean size of 52 mm, started to be recruited. This cohort attained a mean of 68 mm by January 1986.

Females. Females were recognizable at a mantle length of 30 to 40 mm. In March 1985 there was a single size class of females, with a mean at 62 mm. Very few females were caught in May. In June the population developed a pronounced biomodal structure with means at 58 and 103 mm, indicating growth of the 1984 cohort, present in March, and recruitment of a new cohort. By September the 1984 cohort had become extinct and the first 1985 cohort reached a mean mantle length of 85 mm in September. After September the first 1985 cohort became extinct and in November and December a second cohort was recruited with a mean mantle length of 55 mm. This had increased to 63 mm by January 1986.

It is notable that during the year over which the samples were taken, the female population returned to a similar size frequency structure. The males returned to a monomodal structure; the size class of large squid which was present at the start of the sampling programme was absent the following year (Fig. 2).

Maturity stages

The relation between mantle length and maturity stage for all months combined is shown separately for males and females in Fig. 3. There is considerable scatter in the data for males. Although the data for females indicate scatter in mantle length at each maturity stage, there is clearly consistent increase in maturity stage with size.
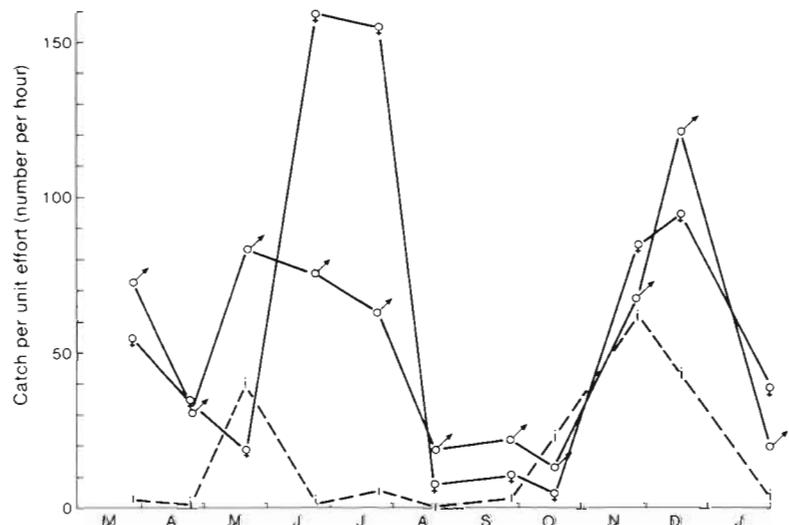
Fig. 1 *Alloteuthis subulata*. Catch per unit effort (no. squid caught per hour) of males (♂), females (♀) and immatures (i)
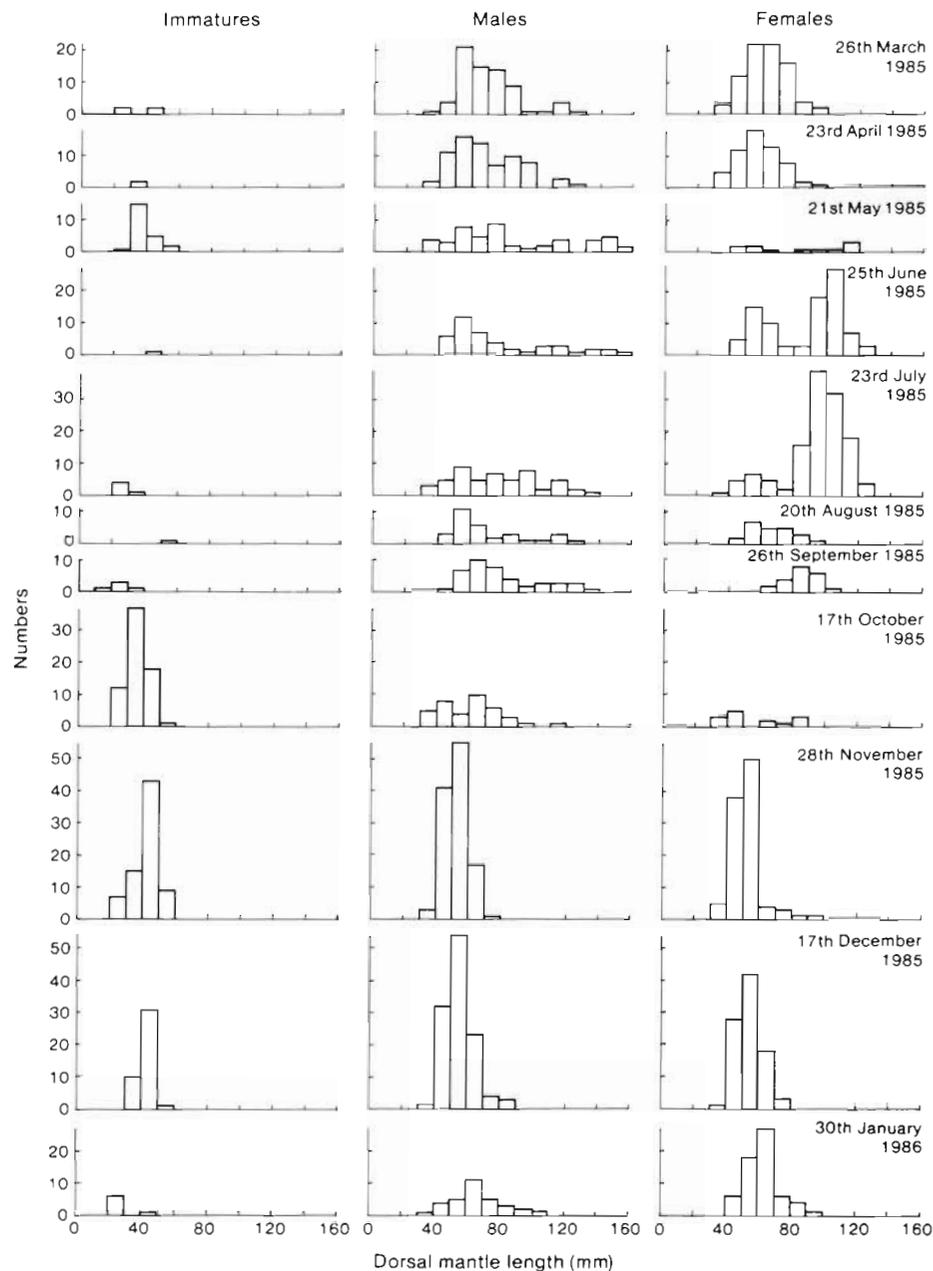
Fig. 2. *Alloteuthis subulata*. Monthly length frequency distributions of immatures, males and female

Allometric relations

Analysis of covariance indicated that there is little evidence for significant difference between months in the relationships between $\log_{10}$ mantle length and $\log_{10}$ total body weight for either sex. The relationships for each sex are well described by the regression equations given in Table 1.

It is notable that for both sexes the exponent (slope) in the equations relating total body weight to mantle length is considerably less than the cubic function

normally associated with length/weight relationships in cephalopods, and somewhat lower than the exponent for other myopsids (Forsythe & Van Heukelem 1987).

Relations between total body weight and gonad weight were determined for each sex, for each month of the year by regression analysis on $\log_{10}$ scale. In females, analysis of covariance showed that the data fall into 2 groups; one regression describes the relation for the period November to January (the 3 mo following the major recruitment of females in 1985) and another
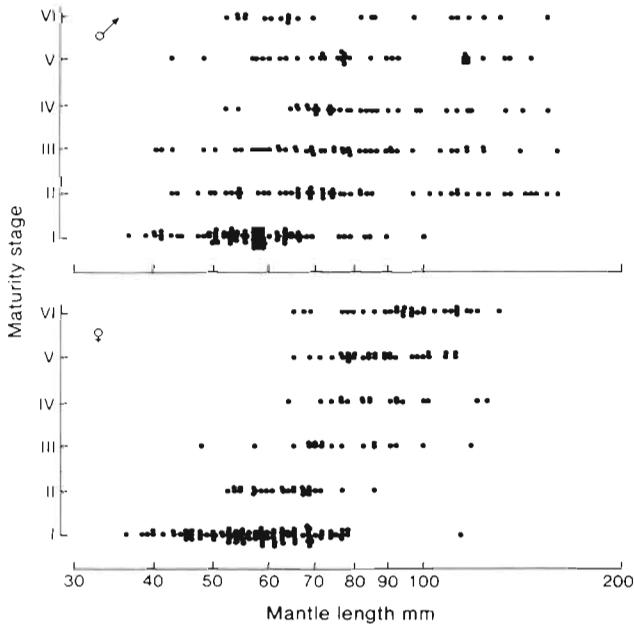
Fig. 3. *Alloteuthis subulata*. Relation between mantle length and maturity stage in males and females

regression describes the relation for the period March to October (Fig. 4). The regression equations are given in Table 1.

The situation is more complex in males because of scatter in gonad weight amaong larger specimens (Fig. 4). A 'broken-stick' model was fitted, for all months

combined, using numerical optimisation facilities in GENSTAT 5. The best estimate for the intersection of the 2 lines is at a total body weight of 1.54 g. Analysis of covariance showed that squid < 1.54 g fall into 2 groups with common slopes but different intercepts (Table 1). One regression describes the relation for the period October to December (following the major recruitment of males in 1985) and another describes the relation for January to September (Fig. 4).

Growth

Males. Growth of males is difficult to interpret during the period March to October. Growth of males recruiting in November/December was similar to growth of females until January although there was greater variance about the mean mantle length. The maximum size attained by males in this population is ca 160 mm mantle length. The disappearance of all sizes of males, apart from recent recruits, in November indicates that the maximum life span is ca 1 yr

Females. The sampling period did not coincide with the beginning and end of the life cycle of the squid and so for the purpose of analysing the growth pattern 2 periods, the first from August 1985 to January 1986 and the second from March 1985 to October 1985, were considered. Mean mantle length ($\pm$SD) for each recognizable size class in Fig. 2, as determined by the 'MIX' programme, is plotted against time in Fig. 5. The early
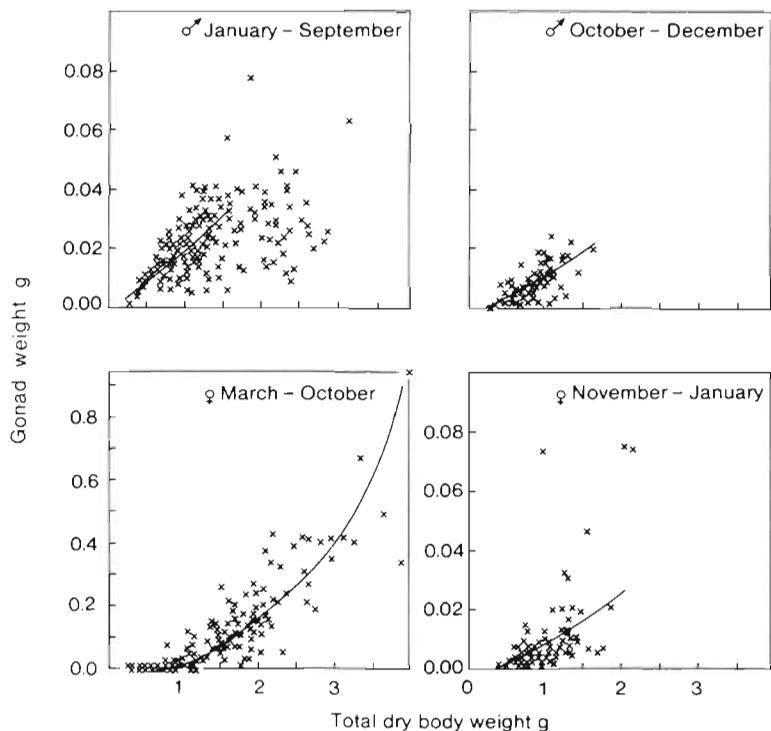
Fig. 4. *Alloteuthis subulata*. Relation between gonad weight and total dry body weight in males and females (curves calculated from fitted $\log_{10}$ models). Curves for males fitted up to body weight of 1.54 g (see text)
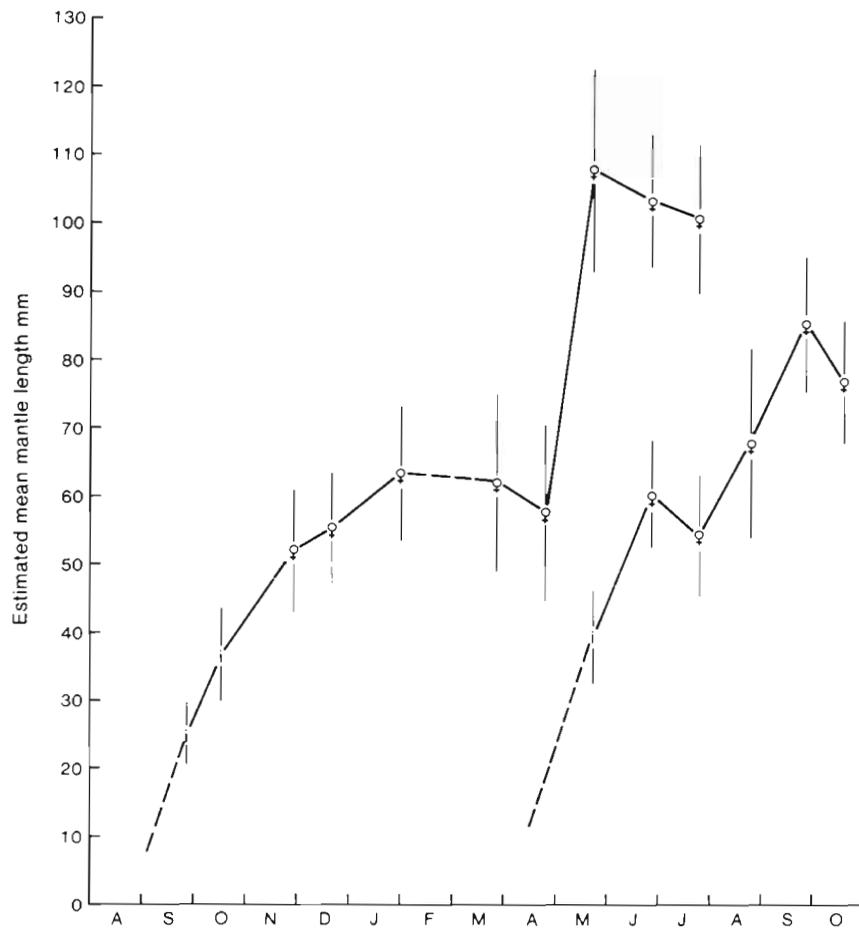
Fig. 5. *Alloteuthis subulata*. Progression of mean length (±SD) in females. The trajectory on the left represents recruits from November/December, that on the right represents recruits from June

parts of the plots include immatures of indeterminate sex.

These curves do not represent individual growth but the progress of the means of each size group, which are influenced by size dependent mortality as well as growth of individuals within the group. The data can be interpreted as follows: the November/December recruited females represent a cohort of squid recruited as immatures over an extended period, October to December, and so include a wide age range. The oldest, and largest, of these spawned during March/April and died, thus causing a reduction in the mean mantle length of the size class, in April. The younger, smaller squid in this cohort, which did not spawn, survived the winter and grew rapidly in the following spring and spawned during the summer, thus giving rise to a further decline in mean mantle length and subsequent extinction of the size class. The June-recruited females, which arose from the March/April spawning, grew rapidly and spawned in October; this spawning was also accompanied by a decrease in

mean mantle length and subsequent extinction of the size class. It was the spawnings by each size class, one in July and the other in October, which gave rise to the extended period of recruitment of females in November and December.

It appears that the maximum length of life for females is 1 yr and that they attain a maximum size of approximately 140 mm mantle length.

Relative growth of gonad and soma

Relative growth of soma and gonad in males and females is shown plotted against mantle length in Fig. 6.

DISCUSSION

The demography of this English Channel population of *Alloteuthis subulata*, especially the male component, was complex during the year sampled. Although the
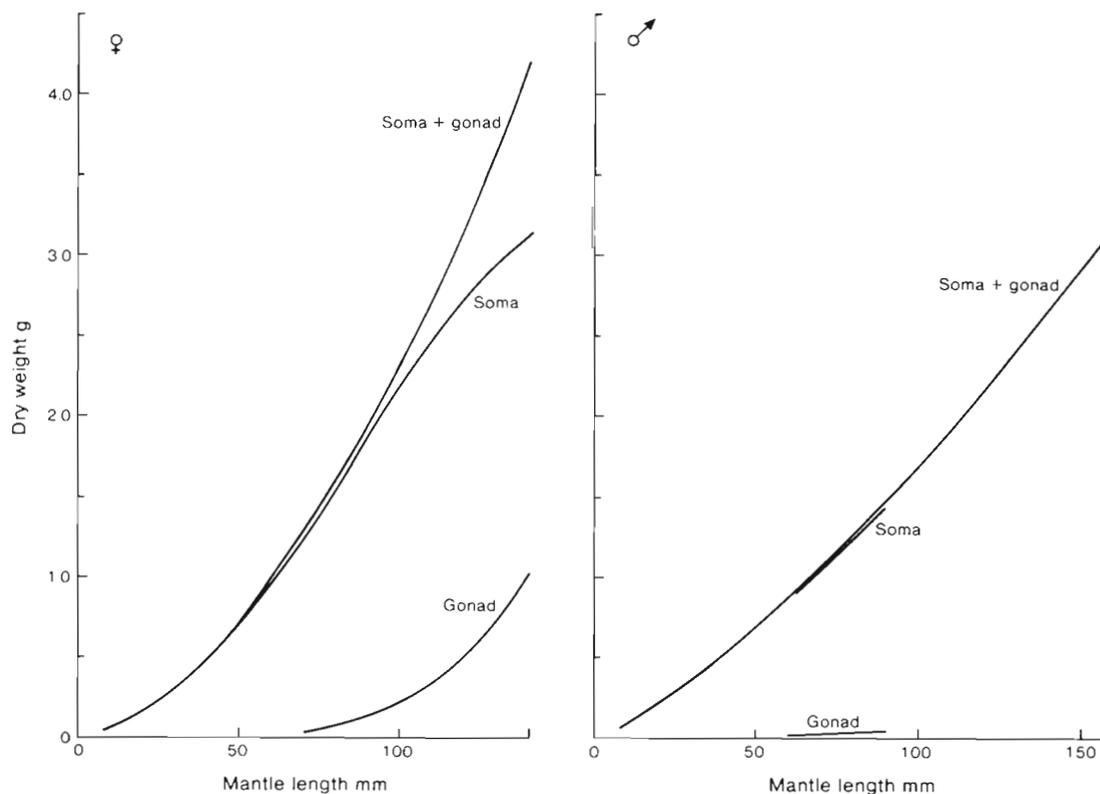
Fig. 6. *Alloteuthis subulata*. Relative growth of total dry body weight, somatic weight and gonad weight in females and males. Females: gonad weight is plotted up to the maximum length attained, 140 mm. Males: gonad weight is plotted up to the intersection of the 2 lines in the 'broken stick' model, 90 mm mantle length (see text)

female population appeared to cycle and return to a steady state after 1 yr, it is not known whether the pattern is constant from year to year. However, several important features of the life cycle were revealed.

The maximum life span of *Alloteuthis subulata* in the English Channel appears to be ca 1 yr. The simple growth pattern of the females makes it easier to follow demographic trends than for the males. Following recruitment females grow to 30 to 40 mm mantle length, at which size they start to mature. Gonad growth commences slowly, then accelerates as maximum length is approached. Because no spent females were caught, it is assumed that spawning is followed soon after by death. In the year of this study there were 3 spawning groups of females, which spawned in the spring, summer and autumn. Clearly a shift in the timing of spawning in any of these groups, mediated by temperature or feeding conditions for example, could cause a different pattern to emerge in subsequent years.

Following recruitment, males grow to 30 to 40 mm mantle length at which size they also start to mature. Unlike females they rapidly attain maturity and can attain stage VI at 50 to 60 mm mantle length (Fig. 3). The allometric relation between testis size and body

size breaks down at a length of about 90 mm suggesting that males start to mate and release spermatophores at a relatively early age, and then continue to mate during the remainder of their life. This is supported by the observation that hectocotylisation takes place in males after attaining a length of 60 mm (Russell 1922). It is not clear whether the poorly defined relation between testis size and body size is due to the testis being slowly, but erratically, depleted during the latter part of life, or whether the testis is regenerated following successive matings.

If, as it appears, males mate repeatedly over an extended period the possibility exists that mating can occur with females from successive cohorts. This would be consistent with the presence of the sexually transmited monogenean parasite *Isancistrum subulatae* in *Alloteuthis subulata* from the sampling area (Llewellyn 1984). This venereal contagion must be transferred from one generation to the next in order to be retained by the population.

The presence during much of the year of females from successive cohorts, in mating condition, has probably resulted in strong inter-sexual selection for early maturation in males. This is in addition to intra-sexual selection pressures which have led to the evolution of

pronounced sexual dimorphism in the species (Roper et al. 1984).

The complexities involved with deriving growth data for females from this population, by cohort analysis, are apparently associated with Lee's phenomenon (Ricker 1975). The fastest growing female squid in a cohort attain full maturity, spawn and die earlier than the slower growing members of the cohort. A growth curve based on progression of the modal size of a cohort will therefore consistently underestimate mean growth rate of squid within a cohort. It will also give an erroneous impression of negative growth during the period leading up to the cohort's extinction. Our inability to derive useful growth data for males is because of the poor definition of cohorts during the summer which is probably due to the confounding effect of interactions between sexual promiscuity, growth rate, and mortality.

In common with some other myopsid squid species (Forsythe & van Heukelem 1987) growth of body length in *Alloteuthis subulata* proceeds at a relatively faster rate than mass. This difference is more pronounced in males, probably because of the development of a long 'tail' in large adults, which increases length with little concomitant increase in weight. In both sexes there has clearly been strong selection for growth in length at the expense of body mass.

Because of the poor relationship between gonad weight and body size in males, due probably to multiple mating, it is not possible to estimate the reproductive investment of males from our data. However, an estimate of reproductive investment by females can be made. Females live for ca 1 yr, spawn once and die, so a measurement of somatic and gonad mass prior to spawning provides an estimate of net lifetime production of both these components of growth. The ratio: $P_r/(P_r + P_g)$ in females that spawn at a maximum size of 140 mm mantle length is 0.25. In other words 25 % of lifetime net production is allocated to gonad growth. Fig. 6 indicates that most of this allocation takes place relatively late in the life of the squid. This measure of reproductive investment does not take into account the metabolic cost of gamete production and it also ignores the exudations of the nidamental and accessory nidamental glands, which provide the egg mass with a gelatinous coating when it is extruded.

The lifetime reproductive investment of *Alloteuthis subulata* (25 % of total tissue production) is less than that of an iteroparous bivalve (57 %) calculated in a comparable way (Rodhouse et al. 1984). It is similar to that of 2 semelparous gastropods and considerably greater than that of a number of iteroparous bivalves at age 12 mo (reviewed by Barber & Blake 1986). The comparatively low investment by *A. subulata*, by comparison with lifetime investment of iteroparous bi-

valves, supports Calow's (1987) conclusion that cephalopod reproductive effort is less than theory would predict for semelparous animals. However, the differences in life style between a pelagic squid and a sessile bivalve suggest that there may be differences in the activity components of the energy budgets of these 2 groups of mollusc. These are not considered in the present analysis. A comprehensive estimate of reproductive effort, including non-reproductive activity and reproductive activity, for example mating behaviour and migrations, might yield a different result but would be technically more difficult to obtain.

Calow (1987) suggests that low reproductive effort in cephalopods may be a reflection of metabolic limitions (O'Dor & Webber 1986, O'Dor & Wells 1987) constraining adaptation of life history patterns (Stearns 1984). Semelparity in cephalopods may be the inevitable consequence of an inability to store metabolic energy reserves other than protein. However, it is not known whether the reliance on protein-based metabolism, which has been described for benthic octopods, extends universally to pelagic cephalopods. High investment in reproduction by a pelagic cephalopod such as *Alloteuthis subulata*, at the expense of production and use of somatic tissue, such as mantle muscle, would entail increased risk of predation through a reduced capacity to escape.

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