

Abstract.—Individuals of the tropical loliginid squid *Photololigo* sp. 1 were collected from the tropical waters of the northwest continental shelf of Australia. Both males and females exhibited pronounced phenotypic variation in size at maturity. Statolith increment analysis was carried out to determine individual age. On the basis of the assumption that statolith increments were deposited daily, counts revealed that this species had a short life-span and that all individuals were younger than 160 d and exhibited linear growth over the size range sampled. All of the longest squid collected were females, which achieved this size disparity predominantly by being older than males rather than by growing at a faster rate. Age analysis revealed that small mature individuals were considerably younger than large mature individuals. A large size distribution of mature individuals was therefore achieved by variation in age at maturity. Possible causal mechanisms are considered.

Variation in size and age at maturity in *Photololigo* (Mollusca: Cephalopoda) from the northwest shelf of Australia

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Pelagic cephalopods are characterized by fast growth, early maturity, and predominantly indeterminate growth (Rodhouse and Hatfield, 1990; Alford and Jackson, 1993). This is especially pronounced in tropical species (Jackson and Choat, 1992). Cephalopods also show considerable variation in individual growth rates (e.g. Natsukari et al., 1988; Jackson, 1989; Arkhipkin and Mikheev, 1992; Villanueva, 1992). Furthermore, a marked plasticity has been noted in size at maturity for a number of cephalopods (e.g. *Lolliguncula brevis*, Hixon, 1980; *Loligo opalescens*, Hixon, 1983; *L. pealei*, Macy, 1982; *Alloteuthis subulata*, Rodhouse et al., 1988; *Dosidicus gigas*, Nesis, 1983; *Sepia officinalis*, Boletzky, 1983; and *Sepia pharaonis*, Dunning et al., 1994). However, whether the variation in size at maturity noted in the above studies reflected age differences or differences in individual growth rate could not be determined because individual age was not known.

Mangold (1983) was able to document not only variation in size at maturity but also variation in age at maturity in the octopus *Eledone moschata* by raising known-age siblings from hatching to maturity. She

found marked differences in sibling growth rates, some siblings showing a tenfold difference in weight after two months. She was also able to document that the differences in size at maturity resulted from some individuals delaying maturation to a greater size and age. Using statolith ageing techniques, Jackson (1993) was able to delineate seasonal differences in trends in gonad growth and age at maturity for field populations of *Loligo chinensis*¹ and *Idiosepius pygmaeus*.

By following the growth of cephalopods of known age in captivity, it is possible to determine whether variation in size at maturity is attributed to differences in individual age or to differences in individual growth and maturity rates or to a combination of both of these factors.

¹ It is now becoming more common to refer to *Loligo* in Australia as *Photololigo* (see Yeatman and Benzie, 1994). The species previously referred to as *Loligo chinensis* (Jackson, 1990b, 1993, 1994; Jackson and Choat, 1992) is now known to be a distinct species inhabiting shallow water in tropical Australia and has been referred to as *Photololigo* sp. 3 (Yeatman and Benzie, 1994) and *Photololigo* cf. *chinensis* (east coast form) in Dunning et al. (1994). Because this species has not yet been named, and to avoid confusion, this species will be referred to by its previously published name.

However, culture conditions do not reflect the natural environment, and although benthic octopods can be raised relatively easily in captivity, this is not true for the pelagic squids. The use of statolith increments to age individual squids is providing a means both to disentangle the size-age question and to determine the reproductive tactics of squid.

During the summer of 1990, collections were made of *Photololigo* sp. 1 from the northwest shelf, western Australia, as part of a population genetic study of Australian loliginids (see Yeatman and Benzie, 1994). This species, which was first identified by using genetic markers, showed marked variation in size at maturity, some individuals maturing at less than half the size of their counterparts. *Photololigo* sp. 1, so named because of the presence of light organs on the ink sac (see Natsukari, 1984), is one of two species identified that fits the gross morphology of *Photololigo edulis* documented from these northern tropical waters (Dunning, 1982). After establishing that the small and large mature individuals do not represent different species (Yeatman and Benzie, 1994), we used statolith ageing techniques on a subsample of these individuals to explore how age is related to the observed plasticity in size at maturity.

Materials and methods

Sample collection

Individuals of *Photololigo* sp. 1 (37 males, 42 females) were collected by bottom trawl during the 1990 September–October cruise of the RV *Southern Surveyor* on the northwest shelf (Fig. 1). After the removal and subsequent freezing of tentacular tissue for electrophoresis, a random subsample ($n=32$) of squid heads was taken from the 79 specimens and fixed in 70% ethyl alcohol. Statoliths were removed from the fixed specimens of *Photololigo* sp. 1 after a period of nearly two years in ethanol. Statoliths of thirteen male squid and nineteen female squid, captured at water depths between 102 and 178 meters, were examined.

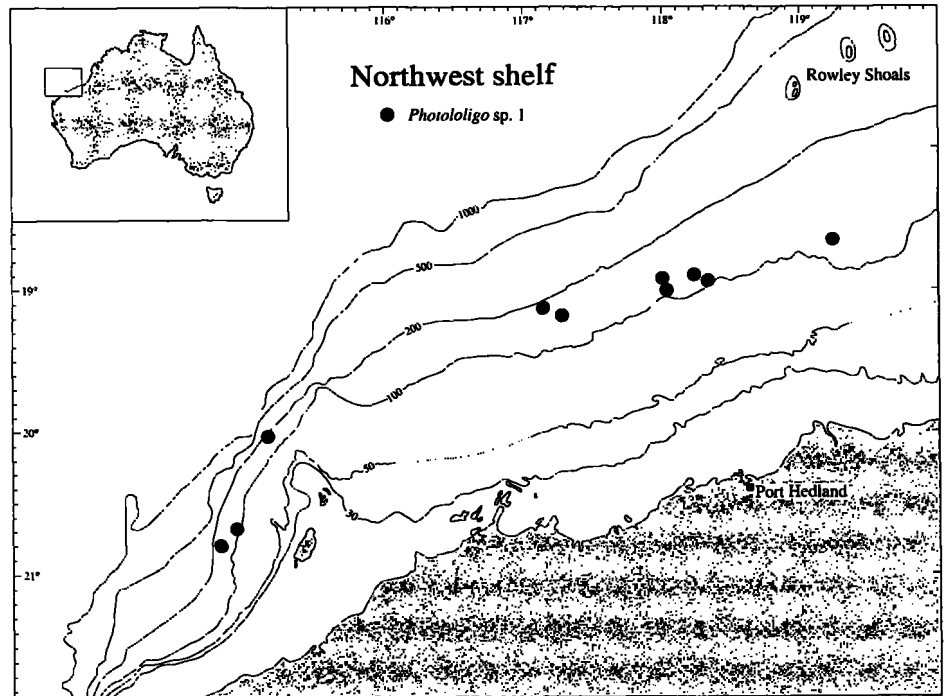


Figure 1

Capture localities for *Photololigo* sp. 1 from the northwest shelf of Australia.

Maturity status

Each squid was assigned a maturity status according to Lipinski's universal scale (see Juanico, 1983; Sauer and Lipinski, 1990) which recognizes six macroscopic stages: 1 = juvenile; 2 = immature; 3 = preparatory; 4 = maturing; 5 = mature; and 6 = spent. For males, the definitions of the various categories are the following: 1 = spermatophoric complex (SC) visible as a spot only; 2 = testes and parts of the SC visible; 3 = spermatophoric organ visible with white streak on vas deferens; 4 = vas deferens extended and spermatophoric sac (SS) contains white particles, testis structure present; 5 = SS contains tightly packed spermatophores; and 6 = degenerating spermatophores and SC, and loss of testis structure.

The categories (stages) in females are distinguished by the following criteria: 1 = nidamental glands (NG) appear as fine transparent strips; 2 = sexual organs translucent or whitish, oviduct meander visible, ovary visible as homogenous structure; 3 = sexual organs not translucent, oviduct meander extended, immature ova visible, NG enlarged; 4 = NG large, covering most internal organs, mature ova in ovary; 5 = same as 4 but mature eggs in oviduct; 6 = few, if any, eggs in the oviduct and ovary.

Lipinski's maturity scale was used because it can easily be used in the field. However, recently stages 1 through 4 have been validated by histological cri-

teria; the differences between stages 4 and 5 were found to be mostly morphological for both sexes (Sauer and Lipinski, 1990). Dorsal mantle length (ML), measured on fresh material, was used as the standard squid length.

Statolith preparation and ageing

Statoliths were stored dry in a plastic cavity block. For increment analysis, statoliths were mounted in the thermoplastic cement Crystal Bond. Increments in statoliths, from small individuals, could be counted directly without any further preparation. The statoliths from larger individuals needed grinding and polishing (see Jackson, 1990a) to reveal all the increments from the nucleus to the edge. The increments within the statolith microstructure were very clear and easy to count. All counts were carried out in the dorsal or lateral region of the dorsal dome by following the increments with a camera lucida attached to an Olympus BH microscope ($\times 400$). Total increment number was taken as the mean of three replicate counts that differed less than 10% from the mean.

The periodicity of the increments was not determined in this study. However, the increments were very similar in appearance to validated daily statolith increments of other tropical loliginids—*Loligo chinensis* and *Loliolus noctiluca* (Jackson, 1990b). Daily periodicity in statolith increments was also validated for the tropical loliginid *Sepioteuthis lessoniana* (Jackson, 1990a; Jackson et al., 1993). The increments within the statolith microstructure of *Photololigo* sp. 1 in this study were therefore assumed to be daily. However, there is a need for validation of increment periodicity in this species.

Results

Photololigo edulis is distinguished from other *Photololigo* species primarily by its sucker dentition, which usually requires detailed morphological inspection. However, previous genetic analysis has revealed two cryptic species exhibiting "edulis-like" teeth in northern Australia (Yeatman and Benzie, 1993).

All of the individuals of *Photololigo* sp. 1 from the northwest shelf in this study were also used in a population genetic study, each for eleven (five polymorphic) loci (Yeatman and Benzie, 1994). Genotypic frequencies for all loci showed good conformance to Hardy-Weinberg expectations for random mating, and the F_{IS} value was not significant, thus demonstrating a lack of within-population structure.

Size at age

The length-at-age data for the *Photololigo* sp. 1 population were linear over the size range sampled. This species appears to have a short life-span; the oldest individual is estimated to be less than 160 d (Fig. 2). The regression equations were $y = 1.12x - 57.46$ [$r^2=0.77$], and $y = 1.02x - 45.57$ [$r^2=0.90$], (where x is age in days and y is ML in mm) for males and females, respectively. Both regressions were highly significant ($P \leq 0.0001$), and there was no significant difference between males and females in the slopes or elevations in the Age:ML relationships (ANCOVA, $P > 0.05$). Males that were aged ranged in size from 38 mm to 87 mm ML, and females that were aged ranged from 32 mm to 115 mm ML.

Maturation

Males All males sampled ($n=37$) were between maturity stages 2 and 5. Stage-5 males showed a large range in mantle length (48 to 126 mm ML). Some mature stage-5 males were smaller than immature stage-3 and stage-4 males (Fig. 3A).

On the basis of the subsample of aged males ($n=13$), the largest male aged was over twice as long as the smallest male aged (Fig. 4A), whereas the oldest male (119 d) was only 31 d older than the youngest male (88 d). The age data (Fig. 4B) confirmed that some males were maturing at not only a smaller size but also at a younger age.

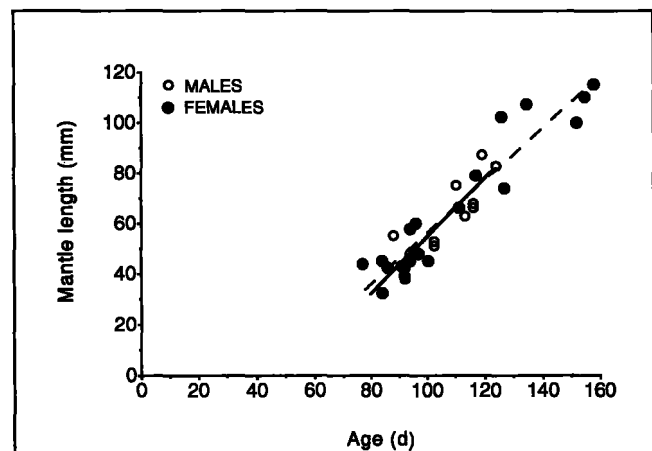
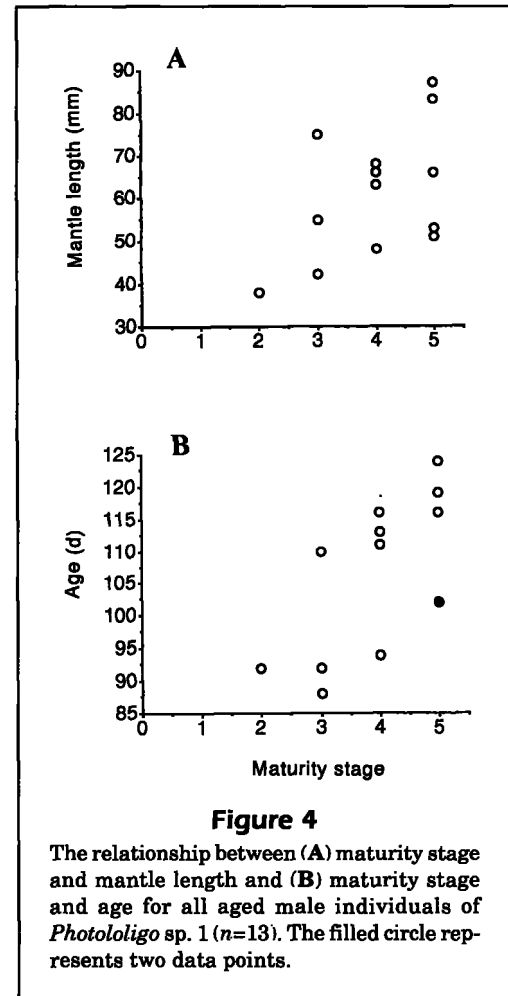
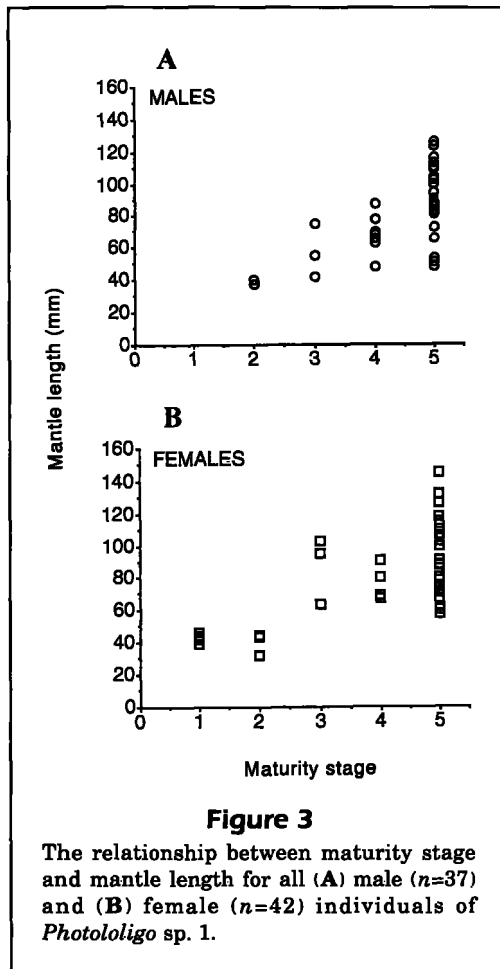


Figure 2

The relationship between age and mantle length for male ($n=13$) and female ($n=19$) individuals of *Photololigo* sp. 1. Solid regression line represents males, dashed regression line represents females.



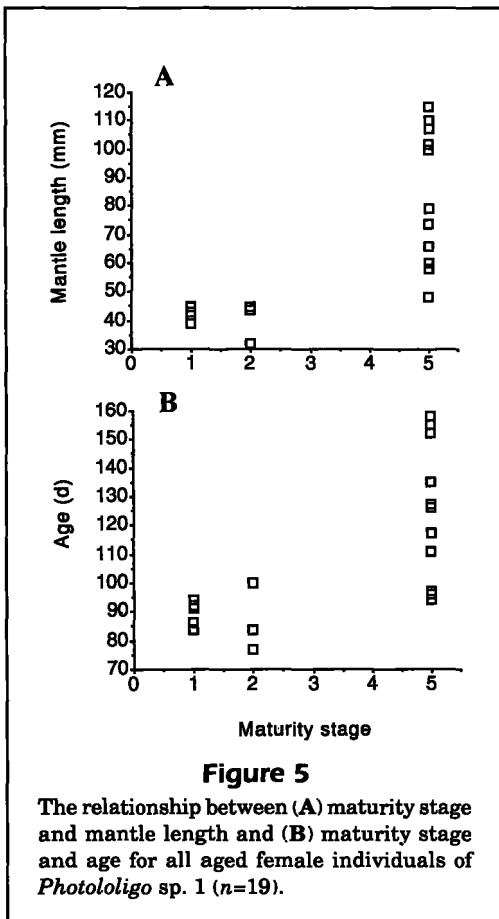
Females There were representatives of all maturity stages in the female sample ($n=42$), with considerable variation in the size of stage-5 females (Fig. 3B). The subsample of aged females ($n=19$) showed pronounced variation in size and age (Fig. 5, A and B) due to the greater size and age of the female sample (age range=77–158 d). The majority of aged females were mature (stage 5) and only eight immature (stage-1 and stage-2) females were available for age analysis. Mature females ranged from 58 mm to 145 mm ML and from 94 to 158 d in age (Fig. 5, A and B). Although all immature females were smaller than the smallest mature female, some of the immature females were actually older than some of the younger mature females. As with the males, the small mature females were not only smaller but younger than their larger mature counterparts.

Discussion

Genetic approaches to squid taxonomy and popula-

tion studies are becoming increasingly important. Electrophoresis has been a successful tool used in the study of population variability within squid species (Carvalho and Pitcher 1989; Garthwaite et al., 1989; Carvalho et al., 1992; Brierley et al., 1993, a and b). Furthermore, genetic techniques are becoming increasingly important as an indispensable tool in taxonomic studies (Brierley and Thorpe, 1994; Yokawa, 1994). Recent work by Yeatman and Benzie (1993, 1994) has demonstrated that electrophoresis can distinguish cryptic species that are difficult to identify morphologically. Continued use of genetic analysis of squid populations is needed and will almost certainly reveal additional cryptic species (e.g. Brierley et al., 1993, a and b).

The short life-span and nonasymptotic growth displayed by *Photololigo* sp. 1 is similar to other tropical cephalopods in northern Australian waters (Jackson and Choat, 1992). This study suggests that there might be sexual dimorphism in *Photololigo* sp. 1, with females obtaining a larger size than males. Other



tropical pelagic cephalopods (e.g. *Idiosepius pygmaeus*, Jackson, 1989; and *Loliolus noctiluca*, Jackson and Choat, 1992) do show sexual dimorphism with females obtaining a larger size and greater age than males. However, this is in contrast to the congener *Loligo chinensis*, males of which obtain a greater length and age (Jackson and Choat, 1992). The ecological or genetic factors contributing to a larger body size in either males or females are currently unclear.

The wide range in age and length at maturity observed in *Photololigo* sp. 1 off northwestern Australia is considerably different from that of the summer population of *L. chinensis* in shallow water off Townsville, North Queensland. Jackson (1993) found that maturation in *L. chinensis* was more closely related to size than age and that individuals reached maturity rapidly over a relatively restricted size range regardless of age. However, Jackson (1993) also found that several of the larger and older females were very immature and thus some individuals did delay maturation. *Photololigo* sp. 1 is a deepwater species captured at depths <100 m whereas *L. chinensis* off Townsville is a shallow water species (generally <20 m and often in <10 m), thus the re-

productive tactics of these two squid species may be a response to the two very different environments.

Considerable variation in size at maturity has also been documented in other loliginids. *Photololigo edulis* in Japan shows considerable variability in size at maturity both geographically and seasonally. Natsukari and Tashiro (1991) have reported mature individuals of *P. edulis* as small as 52 and 59 mm ML for males and females, respectively, whereas the more typical size for maturation is between 150 and 200 mm ML, with some individuals remaining immature until >300 mm ML. *Loligo vulgaris reynaudii* off South Africa can mature as small as 90 and 100 mm ML (males and females, respectively) whereas immature males and females can be as large as 250 and 180 mm ML, respectively (Augustyn et al., 1992). *Loligo gahi* also shows a considerable range in size at maturity, with mature males ranging in size from approximately 71 to >300 mm ML and mature females ranging in size from approximately 98 mm to >220 mm ML (Hatfield et al., 1990). An extreme example has also been recorded by Dunning et al. (1994) who found that all males of the cuttlefish *Sepia pharaonis* collected in the Gulf of Carpentaria, Australia, were mature over a length range of 34 mm to 173 mm ML. These examples of phenotypic plasticity are much more extreme than what has been documented for *Photololigo* sp. 1 in this study. However, by attributing age to individuals, one can consider time-specific aspects in variation in size at maturity.

Considerable phenotypic plasticity has also been observed in some freshwater fishes. Mann and McCart (1981) noted the presence of two forms of *Coregonus sardinella* in a small homogenous lake in northern Canada. The presence of two such morphologically distinct forms was somewhat surprising because of the lack of environmental heterogeneity. The reasons for such plasticity were not discerned, although there was some evidence of spatial segregation and temporal segregation in spawning. Mann and McCart (1981) also suggested that such variation may not be genetically fixed but may rather be a result of different environmental conditions during early development. An even more marked degree of phenotypic plasticity has been observed in the arctic char, *Salvelinus alpinus*, in Thingvallavatn, the largest lake in Iceland. Arctic char occurs in four forms, two planktonic feeders and two benthic feeders (Sandlund et al., 1992). The morphological plasticity in this species appears to be predominantly due to niche separation based on habitat and feeding strategies possibly related to ontogenetic or population divergence.

The phenotypic plasticity observed in *Photololigo* sp. 1 does not appear to be displayed in distinct forms

but rather in a continuum in size and age at maturity from very small, precocious individuals to larger, later-maturing individuals. Such variation appears to be similar to phenotypic variation observed in poeciliid fishes. Poeciliids show a large degree of plasticity in size and age at maturity both within and among populations (e.g. Trexler et al., 1992). Variation in size at maturity for male poeciliids has been related to behavioral interactions such as maturation inhibition due to the presence of larger males or due to environmental stresses such as a limited food supply or a decreased probability of survival (Chapman and Chapman, 1992). Genetic control is also thought to play an important role in variation in size and age at maturity in fish species, with certain alleles causing early maturation in some species of poeciliids (Campton and Gall, 1988).

It is not known whether environmental, behavioral, or genetic factors are influencing the variability observed in size and age at maturity in *Photololigo* sp. 1. It might be a combination of all three factors. Squids exhibit complex behavioral communication and courtship displays (Hanlon et al., 1983; Moynihan, 1985) which in many ways may be analogous to mating strategies in the short-lived poeciliid fishes, which have internal fertilization and the ability to store sperm (Haynes, 1993) as do cephalopods.

The statolith age analysis in this study has revealed that the observed differences in size at maturity were predominantly due to larger individuals being older than their smaller counterparts rather than due to profound differences in individual growth rates. Future work incorporating larger sample sizes of aged individuals will, no doubt, make the discernment of size and age-based patterns of maturity clearer in tropical loliginids.

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