

Abstract.—The age, growth, and reproduction of the tropical Indo-Pacific ommastrephid squid *Nototodarus hawaiiensis* was studied on the North West Slope of Australia. The weight, mantle length (ML), gonad weight, and nidamental gland length were measured for 37 males and 52 females captured in January and February 1992 and ranging in size from 42 mm ML to 214 mm ML. Statolith increments were counted, as a proxy for age. The number of statolith increments, counted on 42 of the squid, ranged from 49 to 195. The relation between increment number (i.e. age) and ML was linear for both sexes. The relation between increment number and ovary weight, and between increment number and testis weight, had greater variability than did ML versus ovary weight, and ML versus testis weight, indicating a large range in age at maturity in individuals of similar size. Some statoliths showed two prominent zones, the origins of which are uncertain. Back-calculated hatch dates indicated that all squid hatched between July and December 1991 and that the majority hatched between August and October (Austral spring).

Age, growth, and reproduction of the tropical squid *Nototodarus hawaiiensis* (Cephalopoda: Ommastrephidae) off the North West Slope of Australia

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Nototodarus hawaiiensis (Berry, 1912) was thought originally to be restricted to the Hawaiian Islands in the central Pacific (Roper et al., 1984). However, studies by Dunning (1988a, 1988b) revealed that this species is also distributed in the Indo-Pacific including the Philippines (previously referred to as *N. sloani philippinensis* [Voss, 1962]), northern Australia, South China Sea, western Indian Ocean, and off Chile (Dunning and Förch, in press). In Australian waters, post-paralarval *N. hawaiiensis* inhabit slope waters at depths between 200 and 500 m off the North West Slope and between 100 and 600 m off the north east coast to southern Queensland (Dunning, 1988b) in bottom temperatures of 12.4°C. Recent trawl surveys on the North West Slope of Australia have shown that *N. hawaiiensis* is the dominant species of cephalopod in commercial catches from demersal trawlers (Wadley, 1993). The recent identification and dominance of *N. hawaiiensis* in waters off the North West Slope of Australia necessitates understanding the biology and role of this species in deepwater marine communities in tropical Australian waters.

This study was carried out to obtain preliminary age, growth, and reproductive parameters for *N. hawaiiensis* not previously reported. Statolith age analysis, a valuable tool in squid growth and life history studies (Jackson, 1994), was carried out as an indication of age and growth. Previous statolith ageing work on tropical Australian squid species has been restricted to shallow water loliginids that predominantly complete their life span in less than 200 d (Jackson, 1990; Jackson and Choat, 1992; Jackson and Yeatman, 1996). However, no growth information has been available to date for deepwater tropical species of other families. It was therefore of interest, for comparative purposes, to obtain life history parameters of this deepwater tropical ommastrephid.

Statoliths of *N. hawaiiensis* were studied to assess if periodic increments might be useful for ageing this species. Owing to the difficulty of obtaining live specimens from deep water, age information has to be inferred (as in this study), rather than validated on living squid. Increment structure was considered in relation to the validation evidence available for other ommastrephids.

Material and methods

Squid collection and analysis

Individuals were collected day and night, 20 January to 14 February 1992, off the North West Slope of Australia, between about 12°S and 22°S (Wadley, 1993) and 385 to 555 m. This study was composed of 89 individuals of which 42 individuals were used for age analysis. Specimens were obtained from the RV *Southern Surveyor* and commercial vessels, which trawled with demersal gear (45-mm mesh net) on soft sandy substrates.

The fresh *N. hawaiiensis* were identified by using field characters from Wadley (1990). Other ommastrephids were captured (Wadley, 1993) but *Nototodarus gouldi* was absent in the area. Specimens were sampled at random from the range of sizes available in the trawl catches. The squid were frozen at sea and subsequently defrosted in the laboratory for reproductive and statolith analysis. Measurements taken included mantle length (ML), total wet weight (W), testis weight for males and ovary weight and nidamental gland length (NGL) for females. Hectocotylisation of the ventral arm and presence of spermatophores in Needham's sac were used as indicators of sexual maturity in males. In females, development of the nidamental gland and presence of mature oocytes in the ovaries were used as indicators of sexual maturity.

Statolith removal and analysis

Statoliths were removed through an incision in the cephalic cartilage, placed singly on microscope slides, and rinsed with 100% ethanol. The dried statoliths were mounted in thermoplastic cement (Crystal Bond, Jackson, 1990). Statoliths were taken for age analysis from 42 individuals selected from the full size range available.

To observe the increment structure, statoliths were ground and polished, usually on both the anterior and posterior surfaces. The complete increment sequence was usually visible only on the posterior (convex) surface, which was preferred for routine counting. In many of the statoliths, the crystal structure obstructed a view of the increments in the nuclear region of the anterior surface. Some statoliths were ground from the anterior (concave) surface through the obstructing crystals until the nucleus was revealed and all the increments could be observed (terminology according to Lipinski et al., 1991).

Statoliths were viewed on a computer monitor with a video camera attached to a compound mi-

croscope. Increments were counted by following the increment sequence with a cursor while using a hand counter. The number of increments on each statolith was counted at least three times and the mean was taken. Counts that varied more than 10% from the mean were repeated or rejected. The increments were similar in structure to daily statolith increments observed in other ommastrephid species (e.g. Hurley et al., 1985; Villanueva, 1992; Arkhipkin, 1996).

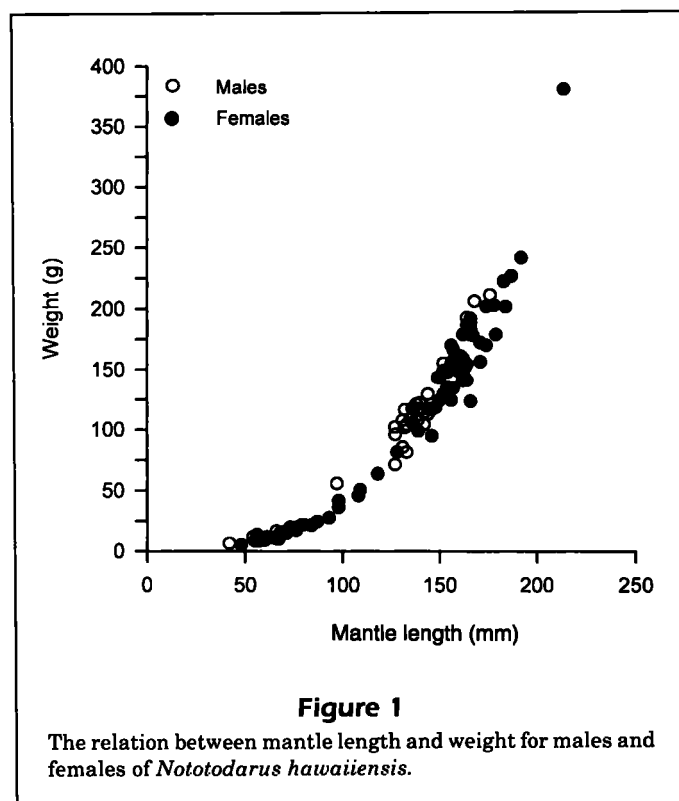
Results

Length-weight relationship

Weight and length parameters were measured for 37 males and 52 females. Males ranged in size from 42 mm ML and 6.6 g to 176 mm and 211.7 g; females ranged from 48 mm ML and 5.3 g to 214 mm ML and 381.6 g (Fig. 1).

Increment number

The relation between the number of statolith increments and ML was linear for both males and females over the size range available, although there was considerable variability in the data (Fig. 2). The regression equations were



$$y = 0.95x - 7.75 \quad (r^2 = 0.75)$$

and

$$y = 1.08x - 14.915 \quad (r^2 = 0.78),$$

for males and females respectively, where x = increment number; and y = mantle length (mm).

The increment count for males ranged from 71 (42 mm ML) to 192 (164 mm ML). Statolith increments in the largest male collected (176 mm ML) could not be counted owing to overgrinding of the statolith. The increment count for females ranged from 49 (48 mm ML) to 195 (183 mm ML). The largest female (214 mm ML) had an increment count of 179.

Male maturation patterns

The largest immature male was 127 mm ML and had 167 statolith increments. Males appeared to mature as early as 100 d and 90 mm ML. Mature males showed considerable range in weights of testis (from 0.92 g to 2.84 g, Fig. 3A).

On the basis of ML alone, testis weight appeared to increase rapidly with growth (Fig. 3A), and there was some evidence of testis regression (on the basis of reduced testis weight relative to ML) at larger

sizes. However, when testis growth was compared with increment number, there was no clear pattern. Plotting testis weight against increment number showed that mature individuals varied widely in age and individuals of similar age varied widely in testis weight (Fig. 3B).

Female maturation patterns

The largest immature female was 166 mm ML and had 192 statolith increments, whereas the smallest mature female was 136 mm ML and had 146 statolith increments. All females larger than 166 mm ML were mature on the basis of the presence of mature oocytes. On the basis of ML (Fig. 4A), females reached full maturity over a narrow length range between approximately 136 and 170 mm ML. However, as with testis weight for the males, ovary weight plotted against increment number (Fig. 4B) showed considerably more variability than did ovary weight plotted against ML (Fig. 4A). The youngest mature female was 125 d. It appeared that there was little growth in the ovary before 100 d.

The largest immature female (166 mm ML) had a NGL of 48 mm ML. Whereas the smallest mature female (136 mm ML) had a NGL of 51 mm, all mature females had a NGL greater than 38 mm. All immature individuals had a NGL less than 50 mm.

The trend in growth of the nidamental gland followed a similar pattern for either ML or increment number (Fig. 5, A and B).

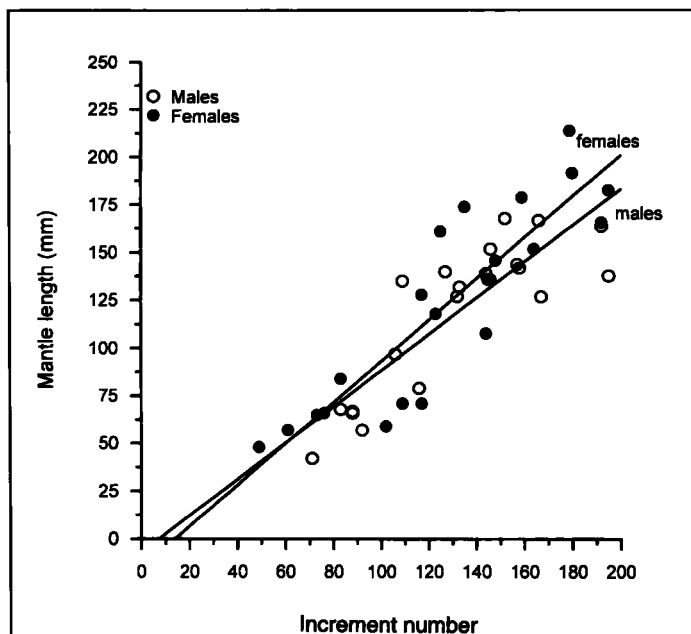


Figure 2

The relation between statolith increment number and mantle length for males and females of *Nototodarus hawaiiensis*. Regression equations are given in the text.

Hatching dates

On the assumption that statolith increments are formed daily, hatching dates were backcalculated. All individuals that were aged hatched between July and December 1991; the majority (83%) hatched between August and November, and 71% hatched in August, September, and October (Fig. 6). Most squid hatched during the austral spring (September–November), although there was some hatching in late winter (July) and early summer (December).

Statolith microstructure and growth zones

The statoliths of *N. hawaiiensis* generally had clear increments that could be counted from the nucleus to the outer margin of the dorsal dome (Fig. 7). There was a pattern in the zonation in nine of the 42 statoliths examined (Fig. 7, A and B). Some individuals had a distinct inner opaque zone followed by an outer translucent zone (Fig.

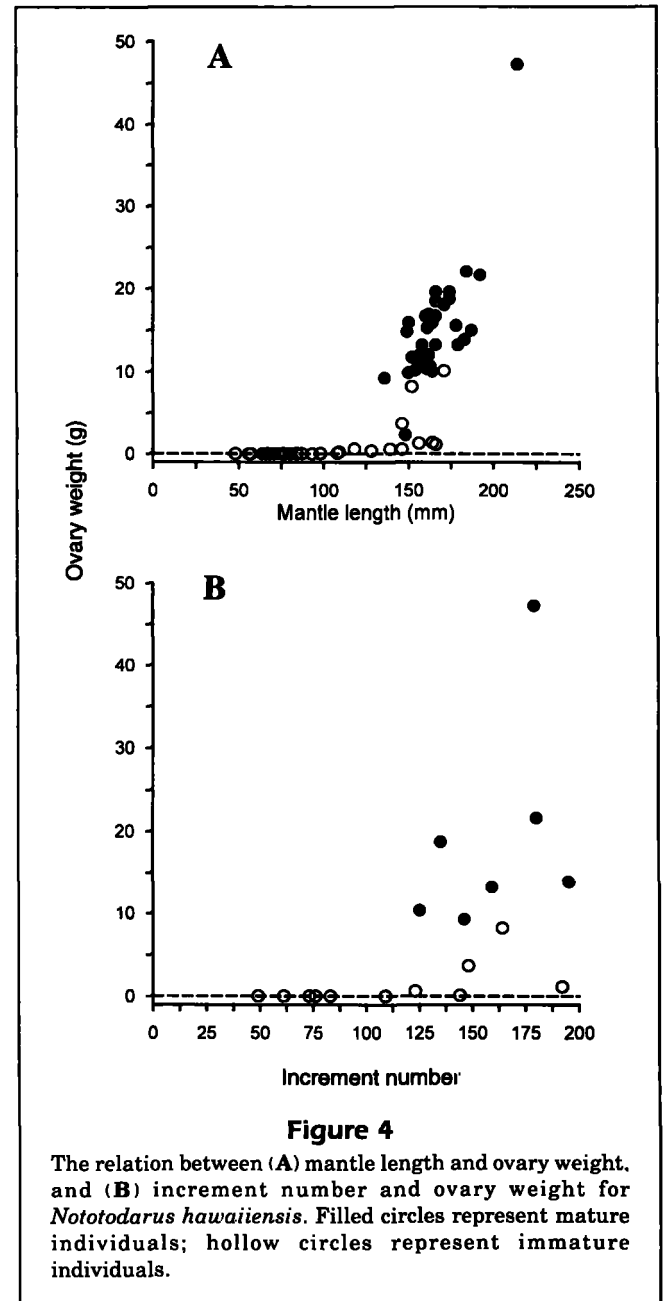
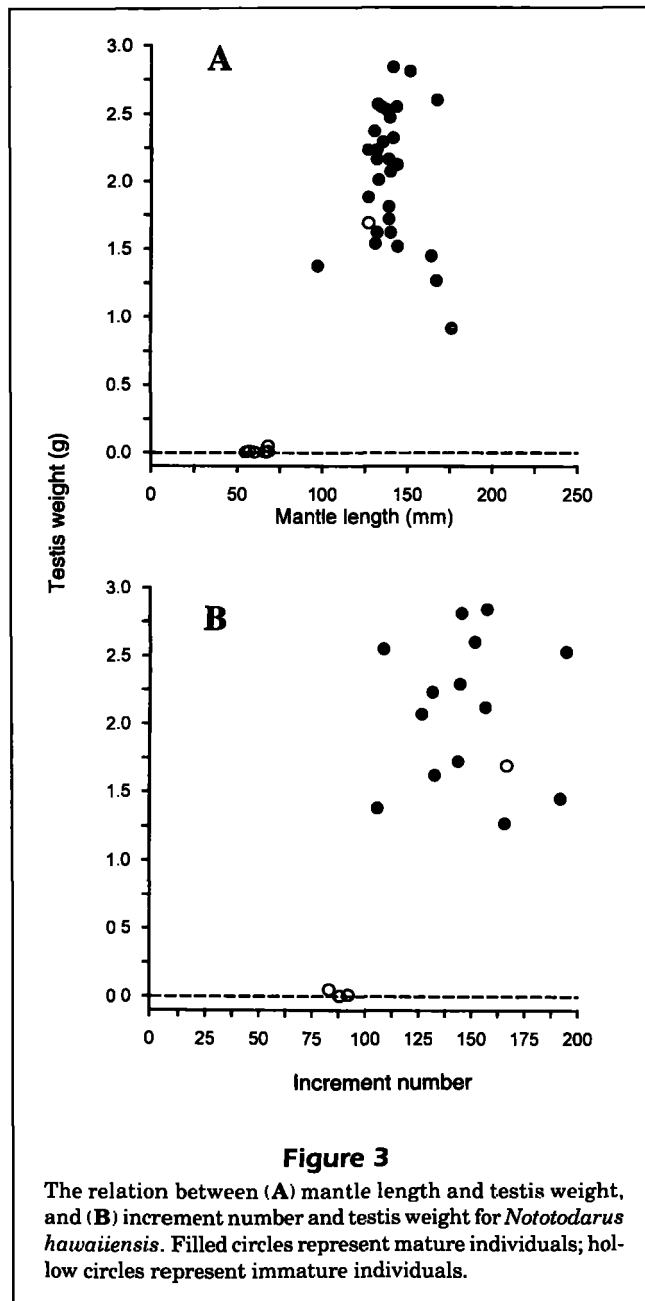
7). No obvious opacity was observed in any of the juvenile (<110 mm ML, $n=14$) statoliths. Opaque zone increment counts on the nine individuals ranged between 89 and 135.

The crystal structure obscuring increments in some statoliths of *N. hawaiiensis* resembled crystals in other squid statoliths. They appeared similar to structures in *Illex illecebrosus*, described as "nodules" by Lipinski (1981) or "occluding crystals" by Dawe et al. (1985). Similar crystals were also observed in the statolith microstructure of the Antarctic squid *Mastigoteuthis psychrophila* (Jackson and Lu, 1994).

Discussion

Maturation

Nototodarus hawaiiensis matures at a relatively young age (<150 d). According to our study of trawl-caught specimens, *N. hawaiiensis* may have a life span of less than 200 d. This is in contrast to its temperate-water conspecifics *Nototodarus gouldi* and *N. sloanii*, which do not reach maturity until 200 d in New Zealand waters (Uozumi et al., 1995). Maturation in *N. hawaiiensis* appears to be more closely tied



to body size than to age, suggesting that there is a minimal physical or physiological size threshold to be reached before maturity can take place, regardless of age. This pattern has also been found in shallow-water *Photololigo* sp. (referred to as *Loligo chinensis* in Jackson, 1993a) and *Lolliguncula brevis* (Jackson et al., 1997), as well as in males of the deepwater onychoteuthid *Moroteuthis ingens* (Jackson, 1997). Guerra and Castro (1994) found that female reproductive organs of *Loligo gahi* generally required a minimum body size before increasing substantially in size. Such a trend may be a common

strategy in squids. *Illex argentinus* in the South Atlantic (Rodhouse and Hatfield, 1990) likewise shows considerable variability in the timing of maturation in relation to age. Rodhouse and Hatfield (1990) postulated that for *I. argentinus*, maturity and gonad growth does not occur at the expense of somatic growth. This also appears to be the case for *N. hawaiiensis*. However, this pattern of maturation contrasts with the deepwater onychoteuthid squid *Moroteuthis ingens*, which undergoes degradation of somatic tissues with maturation (Jackson and Mladenov, 1994).

Size of the nidamental gland relative to body length in *N. hawaiiensis* appears to be a useful indication of female maturity because growth of this organ is closely associated with growth of the ovary (Ikeda et al., 1991, Collins et al., 1995). Uozumi et al. (1995) found a close association in growth of the nidamental gland and ovary size and ovulation in the closely related *Nototodarus sloanii* and *N. gouldi* in New Zealand.

Hatching

Ageing data suggest that some ommastrephids have extended spawning periods (e.g. *Illex argentinus*, Arkhipkin, 1993; *Todarodes pacificus*, Nakamura and Sakurai, 1993; *Todarodes sagittatus*, *Nototodarus sloanii*, Uozumi and Ohara, 1993; *Ommastrephes bartramii*, Bower, 1996). Other ommastrephids, such as *Illex illecebrosus*, which hatches predominantly in spring (Dawe and Beck, 1997), appear to have peaks of spawning. In some instances, spawning peaks may be regionally influenced; *Martialia hyadesi* captured on the Patagonian Shelf Edge had

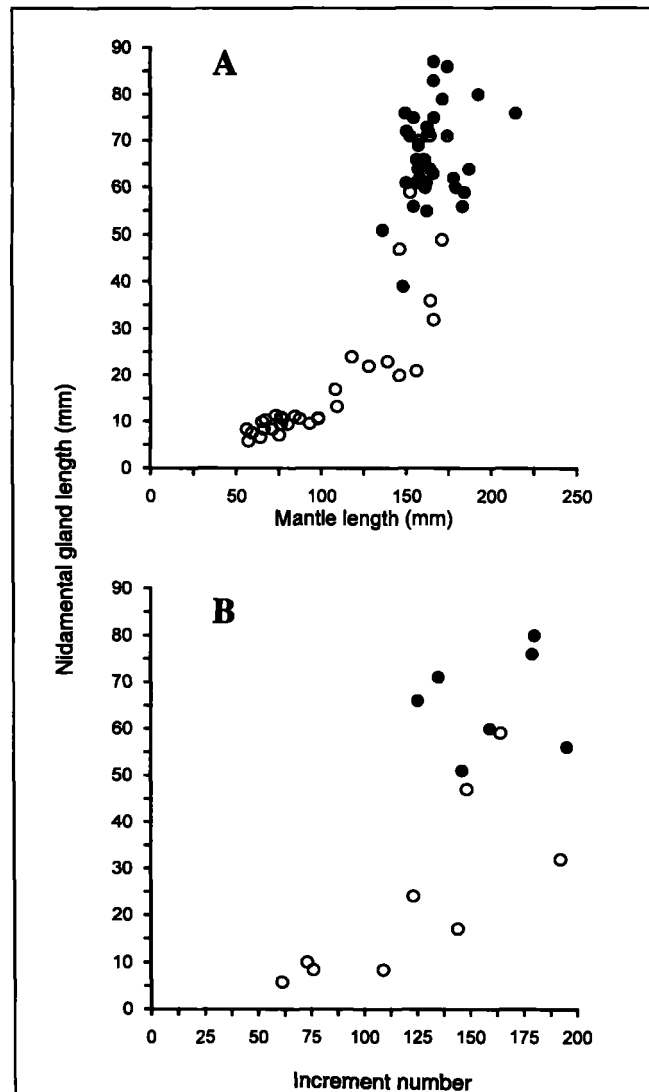


Figure 5

The relation between (A) mantle length and nidamental gland length and (B) increment number and nidamental gland length for *Nototodarus hawaiiensis*. Filled circles represent mature individuals; hollow circles represent immature individuals.

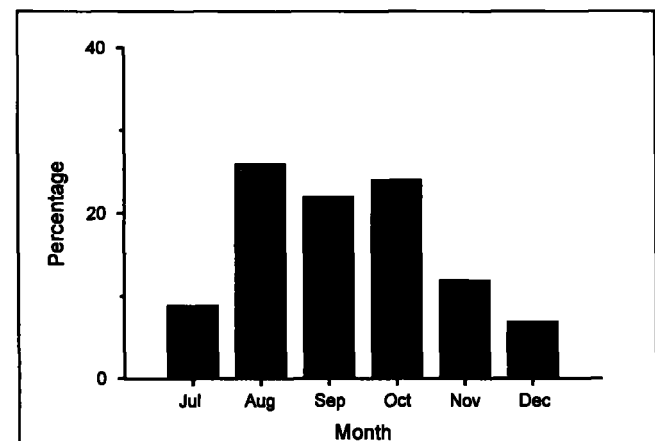
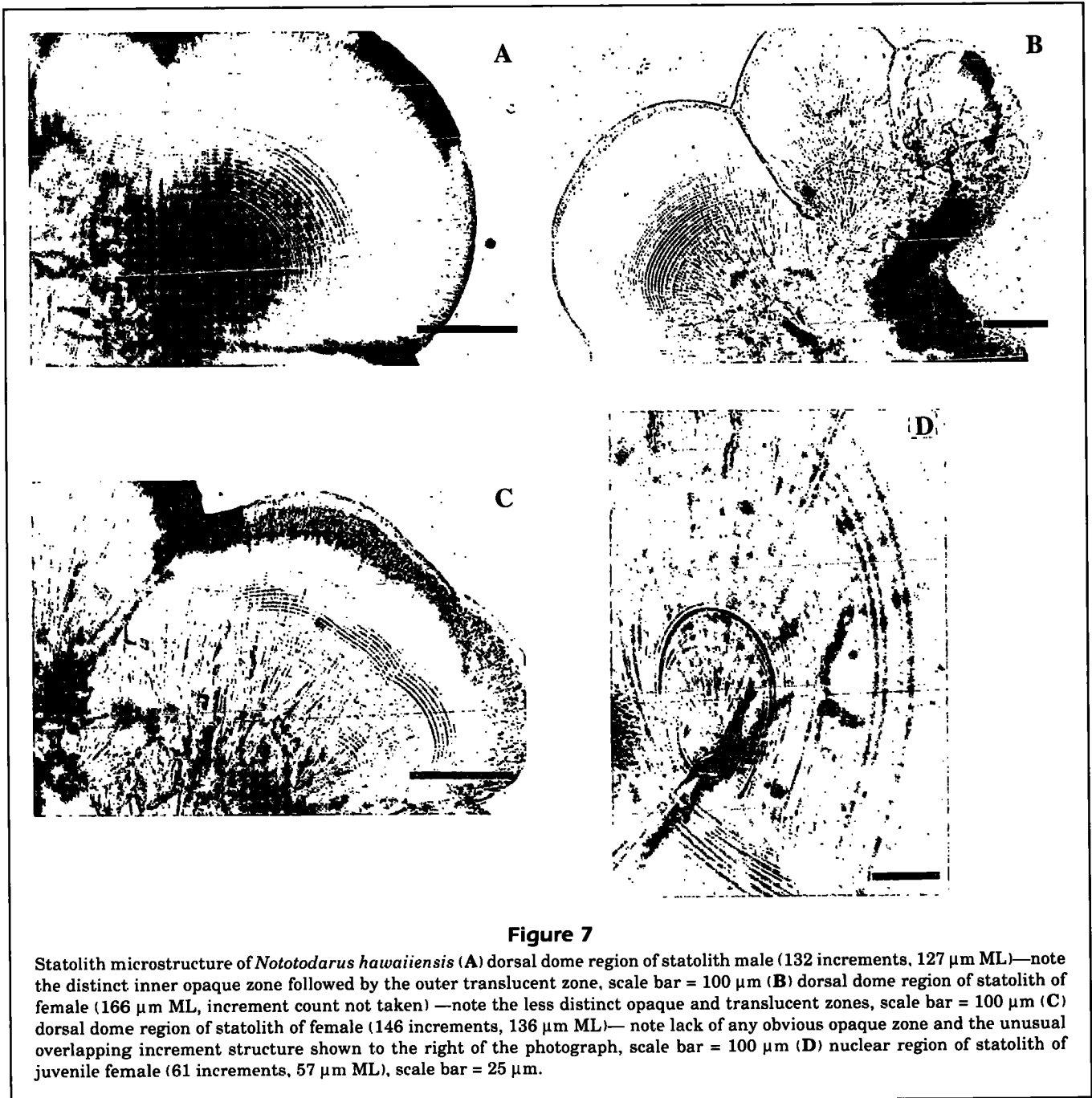


Figure 6

The hatching-date distribution of all individuals ($n=42$) of *Nototodarus hawaiiensis* aged in this study.



a spring peak, whereas individuals captured at the Antarctic Polar Front hatched in winter (Rodhouse et al., 1994). This preliminary data indicates a late winter–spring to early summer hatching for *N. hawaiiensis* in this study. Wadley (1993) collected 50-mm-ML juveniles of *N. hawaiiensis* off the North West Slope in August and 70–80 mm ML juveniles in April, suggesting hatching at different times of the year. From plankton surveys and collection of mature females in North West Slope waters, Dun-

ning (1988a) concluded that *N. hawaiiensis* spawned year-round because paralarvae and juveniles were captured in September and October, and mature females were captured in February, April, August, and late September.

Statolith zones

The origin of the opaque and translucent zones within the statolith microstructure of some of the *N.*

hawaiiensis specimens is unclear. Similar zones that occur in statoliths of the deepwater onychoteuthid *Moroteuthis ingens* might be related to a habitat shift from a pelagic to demersal environment (Jackson, 1993b). The number of increments in the opaque zone was similar for the two species. No zonation was observed in any of 43 statoliths examined from *Nototodarus sloanii* in New Zealand (senior author's personal observ.) which is predominantly a pelagic species. *Nototodarus hawaiiensis* adults are trawled day and night on the seafloor and might be demersal. Pelagic tows at discrete depths would be useful for establishing the ontogenetic descent in this species.

Age and life span of *Nototodarus hawaiiensis*

The deepwater habitat of *N. hawaiiensis* may prevent validation of statolith increment periodicity because of the difficulty of carrying out experiments on live individuals from this habitat. However, some evidence is available on the periodicity of statolith increments in other ommastrephids. Experimental maintenance with chemical markers has shown that statolith increments are laid down daily in the temperate north Atlantic *Illex illecebrosus* (Dawe et al., 1985; Hurley et al., 1985) and in *Todarodes pacificus* in the north Pacific (Nakamura and Sakurai, 1990, 1991). Furthermore, increment counts on successive cohorts suggest that statolith increments are laid down daily in both *Illex argentinus* in the south Atlantic (Uozumi and Shiba, 1993) and in *Nototodarus sloanii* in southern New Zealand waters (Uozumi and Ohara, 1993). We therefore assume that statolith increment periodicity is also daily in *N. hawaiiensis*.

If the assumption of daily periodicity in increment formation for *N. hawaiiensis* is correct, this suggests that the squid matures early and has a short life span. The species reaches maturity in less than 200 d off the Australian North West Slope, considerably earlier than its conspecifics *Nototodarus gouldi* and *N. sloanii* in New Zealand waters, which live for about a year (Uozumi and Ohara, 1993; Uozumi et al., 1995). However, specimens obtained from trawls in this study were smaller than the maximum size recorded for *N. hawaiiensis*. The largest individuals recorded from Australia were 248 mm ML for a female captured off the Northwest Shelf, and 215 mm ML for a male off southern Queensland (Dunning, 1988b; Dunning and Förch, in press). Based on the regressions in Figure 2, and assuming linear growth throughout the life span, the total number of increments even in these larger individuals would be less than 250. However, *N. hawaiiensis* females have been reported to reach 290 mm ML in the western Indian

Ocean and 318 mm ML in the southeastern Pacific. In contrast, individuals of *N. hawaiiensis* are much smaller in the Hawaiian and Philippine waters, with maximum sizes of 180 mm and 160 mm ML, respectively (Dunning and Förch, in press). There thus appear to be regional differences in maximum size (and possibly age) attained by this species.

On the basis of statolith analysis of *N. hawaiiensis* in Australia, this species may complete its life cycle in less than one year. It has a growth rate and life span comparable to tropical Australian shallow-water loliginids, which complete their life cycle in less than 200 d (Jackson, 1990; Jackson and Choat, 1992; Jackson and Yeatman 1996). *Nototodarus hawaiiensis* spends a considerable proportion of its adult life in deeper, cooler waters compared with the loliginids. However, many oceanic squids spend a proportion of their early life phase in the epipelagic zone (Roper and Young, 1975; Vecchione, 1987; Bigelow, 1992). Therefore, a considerable proportion of the life span of *N. hawaiiensis* is probably spent in warmer, epipelagic waters. The youngest individual captured at depth in this study was 49 d, which suggests that perhaps the first 50 days (approximately 25% of the life span) might be spent in the epipelagic zone. Forsythe (1993) proposed a model of squid growth that predicted that increased temperature during a squid's early growth phase can dramatically increase its growth rate, resulting in a much larger adult size. This model has recently been validated by seasonal growth data for *Lolliguncula brevis* (Jackson et al., 1997). *Nototodarus hawaiiensis* may therefore reach a larger size more quickly than if it spent most of its life span in cooler waters at depth.

The statolith analysis of *N. hawaiiensis* on the North West Shelf of Australia suggests a much shorter life span than that of other ommastrephids in tropical waters, e.g. *Todarodes angolensis* in the northern Benguela upwelling (Villanueva, 1992) and *Sthenoteuthis pteropus* in the tropical Atlantic (Arkhipkin and Mikheev, 1992) which have estimated life spans of around one year.

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