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# Hatch Dates and Growth of *Ommastrephes bartramii* Paralarvae from Hawaiian Waters as Determined from Statolith Analysis

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**Abstract:** Planktonic young (paralarvae) of *Ommastrephes bartramii*, have recently been found in early spring (March-May) along the Hawaiian Archipelago. Statoliths of paralarvae ($N = 57$) sampled in February 1991 were used to estimate ages, hatch dates, and growth rates. Growth increments within statoliths were enumerated using light and scanning electron microscopy. Under the assumption that increments were formed daily, paralarvae were estimated to grow exponentially for at least 35 days post-hatching. Based on the growth model, paralarvae 15, 25, and 35 days old had estimated mantle lengths of 1.6, 4.3, and 12.1 mm, respectively. The paralarvae were estimated to have hatched between 1 and 25 January 1991, based on back calculation of statolith increments from the time of capture.

## Introduction

Events occurring during the early life history of squids may profoundly influence their recruitment, for squids are presumably most susceptible to natural mortality during embryonic and paralarval development. The dominant sources of natural mortality in the early life history of marine fishes, and presumably squids, are a combination of density-dependent factors, such as starvation (Lasker, 1975) and predation (Houde, 1987), and density-independent factors, such as temperature and oceanic transport to unfavorable areas (Bailey, 1981; Parrish *et al.*, 1981). Recruitment may be especially influenced by paralarval growth rates which may determine the duration of the paralarval stage: Small declines in paralarval growth rates could result in a longer planktonic period during which high mortality rates are presumed to operate.

Daily growth increments in squid statoliths provide a method for precisely determining the ages, growth rates, and hatch dates of squid from the field. Increment counts have been used to estimate the ages of several squid species and life history stages (see review by Rodhouse and Hatfield, 1990). The daily nature of growth increments has been verified, through laboratory studies, to occur in a variety of teuthoid and sepioid species (e.g., Dawe *et al.*, 1985; Lipiński, 1986; Yang *et al.*, 1986; Jackson, 1989; Nakamura and Sakurai, 1990; Bigelow, 1992), although the physiological mechanisms responsible for increment formation remain obscure (Morris, 1988). Estimation of hatch dates, back calculated from ages at the time of collection, can define periods of successful spawning. Spawning sites may be identified from hatch dates in conjunction with physical data on the rate and direction of ocean currents.

*Ommastrephes bartramii*, is an abundant squid in the subtropical-temperate Pacific Ocean. Since the reduction in stocks of the squid *Todarodes pacificus* in the early 1970's, North Pacific stocks of *O. bartramii* have been targeted by a Japanese jig fishery and by an international driftnet fishery composed of fishermen from Japan, Korea, and Taiwan. Japan's annual catch of *O. bartramii* ranged from 100,000 to 215,000 metric tons between 1981 and 1989, with approximately 80% of the catches taken by the squid driftnet fishery (Murata, 1990; Yatsu *et al.*, in press).

Growth of *O. bartramii* has been estimated from analysis of length-frequency distributions of sequential samples from the jig and driftnet fisheries (e.g., Murakami *et al.*, 1981; Murata *et al.*, 1988). These studies suggest that North Pacific populations are composed of winter and spring cohorts, with a life span of approximately 12–18 months for females and 12 months for males.

*Ommastrephes bartramii* paralarvae are known to occur in two geographical areas: southeast of Honshu, Japan (ca. 35°N, 140°W: Okutani, 1968; 1969), and along the Hawaiian Archipelago (Hayase, 1989; Young and Hirota, 1990). Paralarvae occur in waters off Japan during January, March, April, and May (Okutani, 1968, 1969) and in waters off the Hawaiian Archipelago from at least February to May (Hayase, 1989; Young and Hirota, 1990; R.E. Young pers. comm.). Vertical distribution data suggest that *O. bartramii* paralarvae typically occur at the surface and at 0–40m depth during day and night (Okutani, 1968; Young and Hirota 1990).

Our study examined the growth increments within statoliths of field-caught *O. bartramii* paralarvae (2.1 to 13.7 mm mantle length (ML)) from Hawaiian waters. Using age and hatch-date estimates based on enumeration of growth increments, we estimated paralarval growth rates, defined the periods of successful spawning, and drew inferences about the duration of the paralarval period.

## Materials and Methods

### *Paralarval collections*

*Ommastrephes bartramii* paralarvae were collected during synoptic plankton surveys within 100 nmi of the Hawaiian Archipelago in February 1991 with the NOAA ship *Townsend Cromwell* and the Hokkaido University ship *Hokusei-Maru*. Sampling gear consisted of a 4-$m^2$ ring net, 0.8-$m^2$ ring net, and a Manta neuston net (0.49-$m^2$ mouth)—all with 505 $\mu$m mesh. Oblique tows to approximately 100m were taken with the 4-$m^2$ ring net, and surface tows were taken with the 0.8-$m^2$ ring and Manta nets (Table 1). Paralarval squid were sorted from the plankton on board ship with stereomicroscopes; they were immediately fixed in 95% ethyl alcohol or 99% isopropyl alcohol. Mixed layer temperatures were obtained at each station from conductivity-temperature-depth casts to 1,000m or expendable bathythermograph casts to 700m.

### *Laboratory procedures*

Paralarvae from four locations were used for statolith examination (Table 1). Paralarval identifications followed Young and Hirota (1990) and were confirmed by R. E. Young (University of Hawaii). Dorsal ML and proboscis length of each paralarva was measured to the nearest 0.1 mm with an ocular micrometer and a stereomicroscope. Both statoliths were extracted from the paralarva and placed on microscope slides, then rinsed with distilled water and allowed to dry. Statoliths were mounted in clear resin (Eukitt or Petra-epoxy) with the anterior (concave) side positioned upward. The terminology of Clarke (1978) and Lipinski *et al.* (1991) are used to describe statolith external features and microstructures. Statolith dimensions of focus-dorsal dome length, focus-rostral length, and total length between the dorsal dome and rostrum were measured with an ocular micrometer and compound microscope to the nearest 2 $\mu$m. Microstructural examinations were made with a research-quality compound microscope with transmitted light at magnifications of 600–1500×. Whole statoliths from small ($\leq$6 mm ML) paralarvae were viewed with no further preparation, while statoliths from large (>6 mm ML) paralarvae were ground and polished prior to microscopy to improve increment resolution. Grinding was done by hand rubbing the embedded statolith against fine-grained (1200 grit) sandpaper. The statolith was then polished with 0.3 $\mu$m alumina-silica polishing powder.

For some paralarvae, one statolith of the pair was examined with scanning electron microscopy (SEM) to validate observations made with light microscopy. The lateral dome was ground until the focus was at the ground surface. The surface was polished, etched with 0.1% EDTA for 5–20 minutes, and coated with gold in a vacuum evaporator. Statolith microstructures were viewed and photographed with a Hitachi S-800 SEM at various magnifications (700–5,000×).

An increment under light microscopy consisted of a wide, light ring and a narrow, dark ring, while

**Table 1.** Data on samples of *Ommastrephes bartramii* paralarvae captured and aged from waters around the Hawaiian Archipelago in February 1991.

| Station | Date | Time | Lat. (N) | Long. (W) | Gear | Depth (m) | Temperature (°C) | N | Mantle length (mm) |
|---|---|---|---|---|---|---|---|---|---|
| A1 | 7 Feb | 1553 | 21°56.0′ | 166°52.7′ | 4-$m^2$ ring | 0–100 | 23.8 | 3 | 3.6–4.7 |
| A2 | 7 Feb | 1903 | 21°55.7′ | 167°07.4′ | Manta | 0–1 | 23.8 | 5 | 6.1–13.7 |
| B | 8 Feb | 0930 | 23°04.3′ | 158°57.5′ | 0.8-$m^2$ ring | 0–2 | 22.6 | 36 | 2.1–4.4 |
| C | 13 Feb | 1907 | 25°04.4′ | 163°06.7′ | 4-$m^2$ ring | 0–100 | 21.4 | 6 | 2.8–5.0 |
| D | 15 Feb | 1904 | 23°11.3′ | 161°54.1′ | 4-$m^2$ ring | 0–90 | 23.1 | 7 | 6.5–8.3 |

an increment under SEM. appeared as a wide, lightly etched area (light ring) and a narrow, deeply etched area (dark ring). For each microscopy method, statolith increment counts were made independently by each author at four separate reading sessions.

## Results

Microstructural examination revealed a conspicuous, dark, elliptical zone in the interior of all statoliths under light and SEM (Figs. 1–3). Under SEM, the long axis of the ellipse averaged 21.8 μm (SD = 3.4 μm, $N = 17$), while the short axis averaged 17.4 μm (SD = 2.8 μm, $N = 17$). This distinctive zone was postulated to be the statolith size at hatching or natal size, because of the similarity in size to *Illex illecebrosus* (Balch *et al.*, 1988) and *Abralia trigonura* (Bigelow, 1992). In the microstructural examination, two features influenced increment enumeration. Weak increments were present between more typical increments on the dorsal dome in a zone of progressively increasing increment width. Increments bordered by distinct, deeply etched, dark rings were presumed to be daily (Fig. 4A), while subdaily increments were defined by faint, shallowly etched, dark rings (Fig. 4B). A second feature influencing increment enumeration was about a 10- to 15-μm area, immediately distal to the natal ring, that lacked any consistent structuring (Fig. 3). As a matter of convention, increments were enumerated based on continuity of increment width with adjacent increments. The magnitude of the count bias associated with unresolved growth increments appeared to be small, because increment widths of 3-4.5 μm were extrapolated over an unresolved area of 10–15 μm. Interpretation of the remainder of the statolith was largely unambiguous. In both microscopy methods, increments were always enumerated from the natal ring to the lateral dome (Figs. 1–2), as statolith orientation was not sufficient to allow increment counts on the rostrum or dorsal dome.

Statoliths were examined with light microscopy from 57 paralarvae of 2.1–13.7 mm ML. A paired $t$-test showed a significant difference between the mean increment counts of the two readers ($p < 0.05$). Mean difference between readers was 2.6 increments. For both readers, no significant difference was found between mean counts of paired statoliths from the 47 paralarvae in which both statoliths were extracted (one-way analysis of variance, $p > 0.05$).

Statoliths from 24 paralarvae were examined with SEM. Mean difference between readers was 0.9 increments. Contrary to mean increment counts from light microscopy, there was no significant differ-

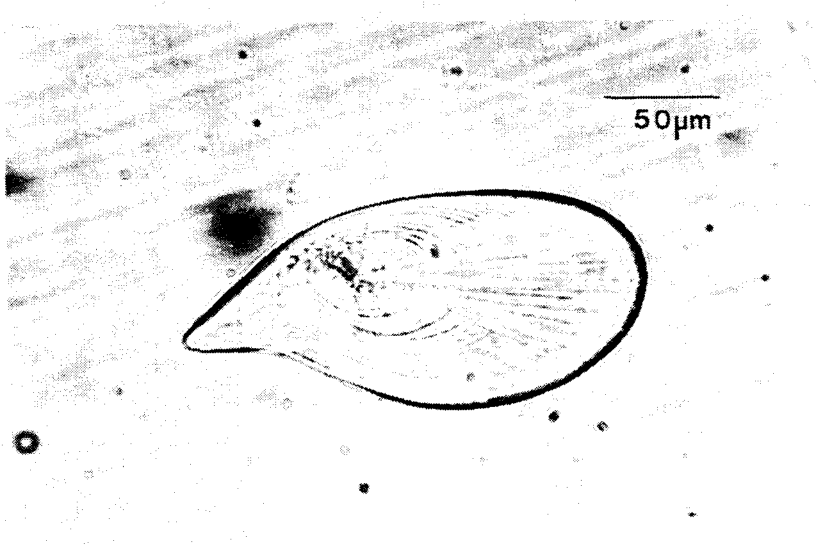

**Fig. 1.** *Ommastrephes bartramii.* Light micrograph of a statolith from a 2.5 mm mantle length paralarva used for increment enumeration.

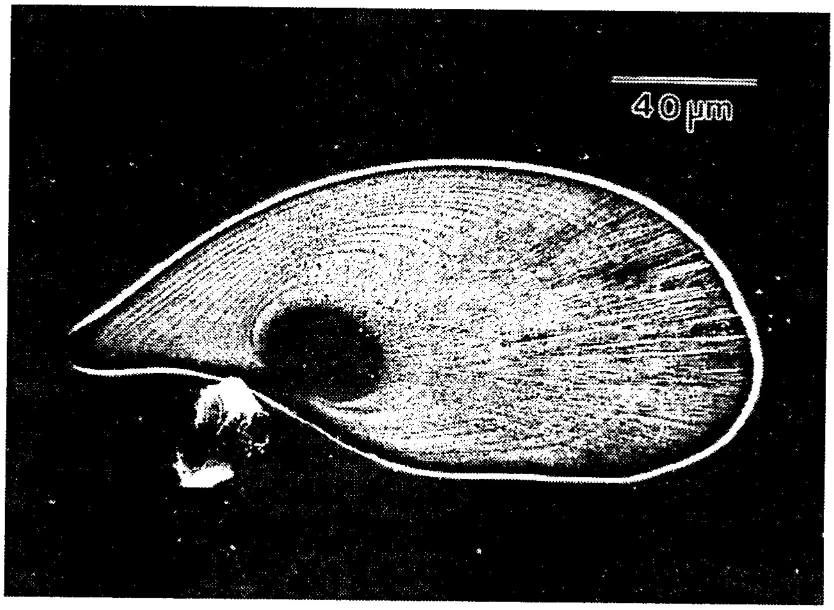

**Fig. 2.** *Ommastrephes bartramii.* Scanning electron micrograph of a ground and etched statolith from a 2.5 mm mantle length paralarva used for increment enumeration.

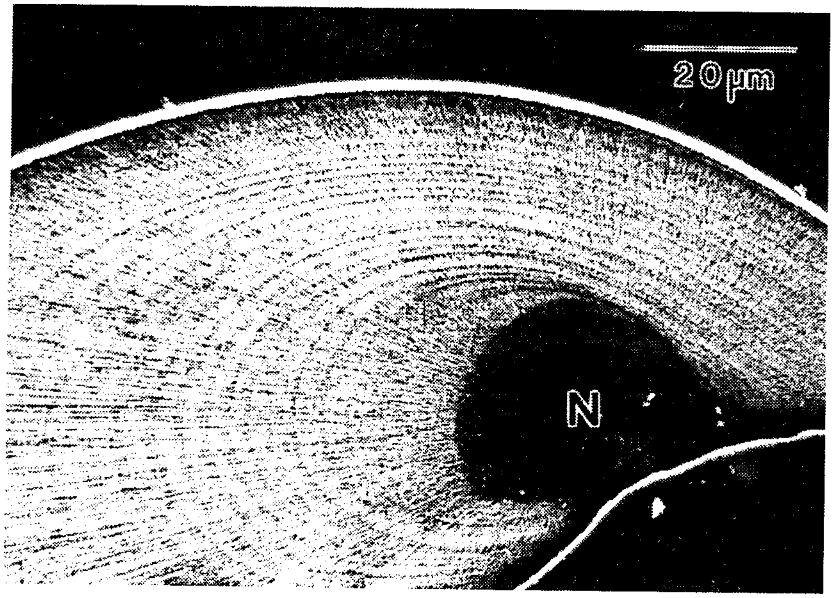

**Fig. 3.** *Ommastrephes bartramii.* Scanning electron micrograph of a ground and etched statolith from a 5.0 mm mantle length paralarva, which demonstrated a nucleus (N).

ence between mean SEM counts of the two readers ($p > 0.05$). No significant difference was found between pooled increment counts from light microscopy and SEM ($p > 0.05$). Differences in increment counts between readers were greater with light microscopy compared to SEM, because under light microscopy, microstructures around the natal zone were difficult to resolve and subdaily increments were more prominent.

For each paralarva, increment counts of both readers made with light microscopy were averaged for analysis of growth in length. An increase in squid size and increment number resulted in an increase in all statolith dimensions (Fig. 5A-B). Increment at length data were pooled over all stations and the following exponential model was fit to the data:

$$ML = 0.331e^{(0.103x)}$$

where ML is in millimeters and $x$ equals the mean increment count (Fig. 6). Nonlinear regression parameters were estimated by least-squares methods. Coefficient of determination ($r^2$) was 0.92. Deviations from the model included individual variability in growth of a paralarva, error in ML measurements, and error in increment counting. Residuals exhibited no conspicuous systematic deviation from linearity by sampling site and no marked increase in variance with age. There were too few samples to test for differences in growth rates between stations. Based on the growth model, paralarvae at an age of 15 days post-hatching (1.6 mm ML) grew at a rate of 0.16 mm·day$^{-1}$, whereas the growth rate of 35-day-old paralarvae (12.1 mm ML) was 1.25 mm·day$^{-1}$ (Table 2). Paralarval length at time of hatching was estimated to be 0.33 mm ML.

The proboscis of *O. bartramii* started dividing by about 6 mm ML (Fig. 7). Proboscis division was completed between 9.5 and 12.0 mm ML, which corresponds to an age range of 32–35 days.

Hatch dates were back calculated through the subtraction of the paralarval age from the date of collection, and were pooled into 3-day periods (Fig. 8). Samples were not pooled because paralarvae were collected with different net types over a large geographical area. The hatching period was 1–25 January 1991. At stations B, C, and D, paralarval hatch dates occurred over a narrow range of 8 days, while paralarvae sampled at station A hatched over a period of 16 days. Paralarvae collected at stations B and D had similar hatch dates (12–19 January 1991).

## Discussion

Analysis of statolith microstructures allowed us to realistically estimate the growth and hatch dates of

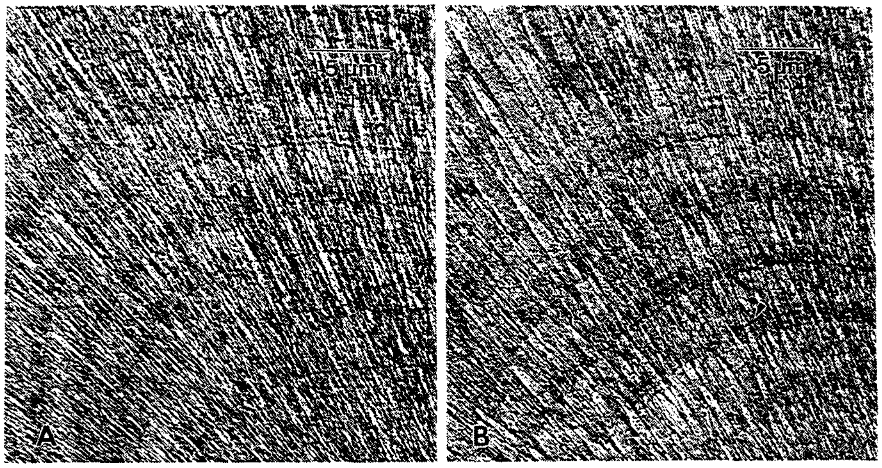

**Fig. 4.** *Ommastrephes bartramii.* Scanning electron micrograph of increments within a statolith. (A) Daily increments were bordered by deeply etched, dark rings. (B) Subdaily increments were composed of faint, shallowly etched, dark rings (arrow).

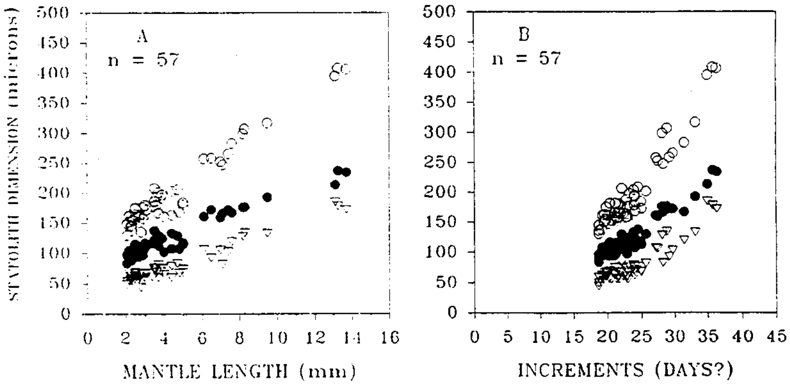

**Fig. 5.** *Ommastrephes bartramii.* Relationship between (A) statolith dimensions and mantle length of paralarvae, and (B) statolith dimensions and number of growth increments (open circles indicate statolith total length; closed circles, focus-dorsal dome length; and triangles, focus-rostral length).

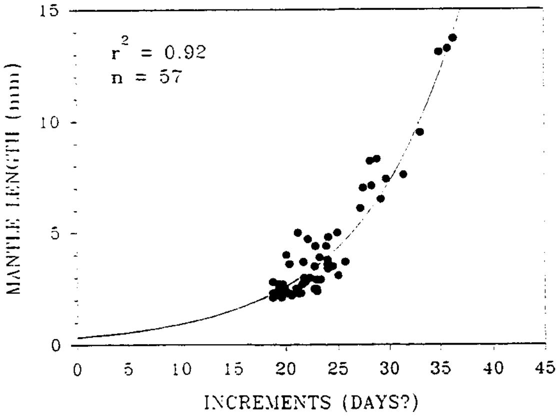

**Fig. 6.** *Ommastrephes bartramii.* Relationship between mantle length and number of increments in statoliths. Exponential growth curve was based on increment counts from statoliths of 57 specimens viewed with light microscopy.

*O. bartramii* paralarvae. A primary assumption of statolith microstructural analysis is that growth increments are formed daily. Growth increments of *O. bartramii* paralarvae are assumed to be daily, based on the similarity in increment appearance in previous studies that validated the frequency of increment deposition (e.g., Dawe *et al.*, 1985; Bigelow, 1992). Validation experiments are impossible at present because eggs, presumably laid in masses, have never been captured and field-caught individuals are not amenable to statolith marking experiments for they perish quickly in captivity. Although we did not validate the frequency of increment deposition, previous studies have for two orders of cephalopods (Teuthoidea and Sepioidea) (e.g., Dawe *et al.*, 1985; Lipiński, 1986; Yang *et al.*, 1986; Jackson, 1989; Nakamura and Sakurai, 1990; Bigelow, 1992), which suggests that daily increment formation may be common to many cephalopod species. However, the existence of subdaily increments in *O. bartramii* statoliths and other squids (Jackson, 1990; Bigelow, 1992) may be a potential source of error if im-

**Table 2.** Comparison of paralarval growth in mantle length (ML) of three ommastrephids based on presumed daily growth increments within statoliths

| | Age | | | | | |
|---|---|---|---|---|---|---|
| | Day 15 | | Day 25 | | Day 35 | |
| | Size ML (mm) | Growth (mm/day) | Size ML (mm) | Growth (mm/day) | Size ML (mm) | Growth (mm/day) |
| *Ommastrephes bartramii*[a] | 1.6 | 0.16 | 4.3 | 0.45 | 12.1 | 1.25 |
| *Illex illecebrosus*[b] | 1.8 | 0.08 | 2.7 | 0.11 | 4.2 | 0.17 |
| *Stenoteuthis oualaniensis*[c] | 2.4 | 0.08 | 3.4 | 0.11 | 4.8 | 0.16 |

[a] From the present study; [b] From Balch *et al.* (1988); [c] From Bigelow (1991).

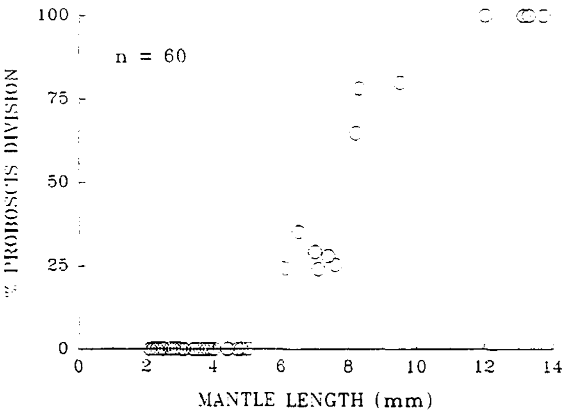

**Fig. 7.** *Ommastrephes bartramii.* State of proboscis division by mantle length.

properly interpreted. A second source of error in interpretation is the presence of an area immediately distal to the natal zone which lacked any consistent structure. Difficulty in resolving increments near the natal ring has been documented for a number of squid species (e.g., Dawe *et al.*, 1985; Jackson, 1989; Bigelow, 1991). Presumably, this ambiguous area corresponds to the yolk stage within early life history. Cues for increment deposition, such as feeding cycles, may not be as strong in the yolk stage and may result in poorly defined increments.

Paralarval growth in length of various squids typically conforms to exponential equations (e.g., Balch *et al.*, 1988; Forsythe and Hanlon, 1989; Bigelow, 1991). Paralarval growth in length of *O. bartramii* is also characterized as exponential for at least 35 days post-hatching. The derived estimate of hatching size (0.33 mm ML) from the growth model is probably underestimated. Although the hatching size of *O. bartramii* is unknown, the size may be approximately 1 mm ML, because other confamilial species are known to hatch at this size [*Todarodes pacificus*, 1.2 mm ML (Hayashi, 1960); *Illex illecebrosus*, 1.2 mm ML (O'Dor *et al.*, 1982)], and Young and Hirota (1990) captured a yolk-stage paralarva which was approximately 1.0 mm ML. In the future, smaller (1–2 mm ML) paralarvae may be captured, and age at length estimates may provide a model which extrapolates to a realistic estimate of ML at hatching.

Our paralarval growth rates are comparable to growth estimates of confamilial species. Paralarval growth derived from statolith analysis has been estimated for *I. illecebrosus* captured from the Gulf Stream off Florida (Balch *et al.*, 1988) and *Stenoteuthis oualaniensis* from Hawaiian waters (Bigelow,

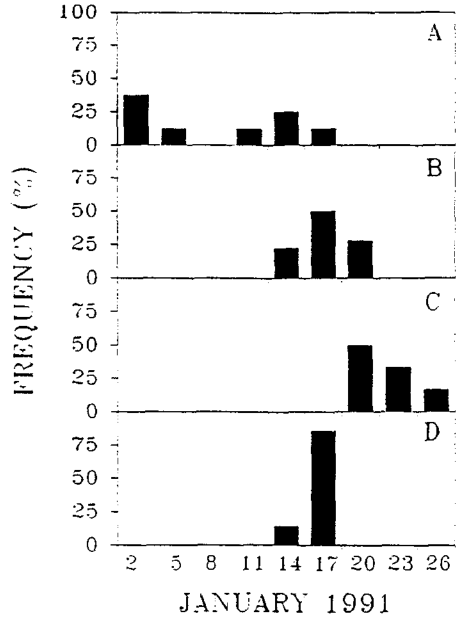

**Fig. 8.** *Ommastrephes bartramii.* Hatch-date distributions derived from examination of statolith microstructures. Stations A, B, C, and D correspond to collection sites in Table 1.

1991). The ML at age estimates were modeled for the three species (Table 2). Though temperature and food effects are unknown, *O. bartramii* paralarvae grew the fastest, while *I. illecebrosus* and *S. oualaniensis* paralarvae grew at similar rates. Since temperature can affect paralarval growth rates (Forsythe and Hanlon, 1989), an age- and temperature-based growth model similar to that recently developed for fish larvae (Campana and Hurley, 1989) could be applied in future comparisons of paralarval growth rates.

The paralarval stage of the Ommastrephid family is classically considered to end with the division of the proboscis to separate the tentacles and is therefore referred to as the rhynchoteuthion stage. A change in statolith growth axes has been postulated to coincide with a transition in life history stages of some squid (Morris and Aldrich, 1985; Bigelow, 1992). For *I. illecebrosus*, the splitting of the proboscis is complete by 8–10 mm ML (O'Dor, 1983). Based on a change in statolith form at about 50 mm ML, Morris and Aldrich (1985) suggested that the paralarval stage extends beyond the rhynchoteuthion stage in *I. illecebrosus*. For *O. bartramii*, the division of the proboscis is complete at 9.5–12.0 mm ML, though there was no change in statolith dimensions at the end of the rhynchoteuthion stage. Therefore, we concur with Morris and Aldrich (1985) in suggesting that the paralarval stage of *O. bartramii* may extend beyond the rhynchoteuthion stage.

The ages of *O. bartramii* paralarvae in our study indicate a hatching period between 1 and 25 January. *Ommastrephes bartramii* paralarvae (6–8 mm ML) have been captured from Hawaiian waters as late as 5 May (Hayase, 1989). Assuming a growth rate similar to the present study, the paralarvae sampled by Hayase (1989) would have hatched between 5 and 7 April. The apparently protracted spawning period concurs with present theories (see review by Murata, 1990) that North Pacific stocks of *O. bartramii* are composed of cohorts spawned during winter and spring.

Statolith analyses are invaluable to ecological and population studies, as they supply the cephalopod biologist with a technique to resolve life history information on a daily level. Future studies with larger sample sizes of *O. bartramii* paralarvae may reveal the environmental conditions which are favorable for paralarval growth and survival.

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