Abstract.— Statolith micro-structural analysis was applied to 126 specimens of the oceanic boreal clubhook squid, *Onychoteuthis borealijaponica*, for estimation of age and growth rates. Specimens were captured from the western, central, and eastern North Pacific between approximately lat. 38° N and 47°N by driftnet fishing, trawling, and jigging in the summers of 1990 and 1991. Results suggest that increments were deposited at a rate of one per day. Both sexes live approximately one year; males mature at smaller sizes and younger ages than females. Exponential growth models suggest that growth in length was similar for males and females (0.80% ML/day) in the central North Pacific, while growth in weight was higher for females (1.90% WT/day) than males (1.40% WT/day). Females in the western North Pacific exhibited faster growth rates than individuals from the central North Pacific. *O. borealijaponica* were estimated to have hatched year round based on back calculation of statolith increments from the time of capture. Post-recruit individuals exploited in the *O. borealijaponica* jig fishery and *Ommastrephes bartramii* driftnet fishery typically hatched from late summer to early winter.

Age and growth of the oceanic squid *Onychoteuthis borealijaponica* in the North Pacific

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The oceanic boreal clubhook squid *Onychoteuthis borealijaponica* Okada, 1927 is common in subarctic waters of the North Pacific. This species ranges from the western coast of the United States and Canada to the eastern coast of Hokkaido, Japan, and the Kurile Islands, but does not occur in the Sea of Okhotsk or Bering Sea (Young, 1972; Murata et al., 1976; Naito et al., 1977a; Fiscus and Mercer, 1982; and Kubodera et al., 1983). *Onychoteuthis borealijaponica* has commercial value throughout its range. Between 1971 and 1979, commercial landings averaged 1,171 metric tons (t) per year from a jig fishery in oceanic waters east of Hokkaido, Japan (Okutani and Murata, 1983), and approximately 254 and 2,705 t of *O. borealijaponica* were caught in 1990 and 1991, respectively, by Japan, Korea, and Taiwan in the *Ommastrephes bartramii* highseas driftnet fishery (DiNardo and Kwok, in review[1]). Based on exploratory fishing, Fiscus and Mercer (1982) suggested that *O. borealijaponica* could be commercially exploited by a jig fishery from the Gulf of Alaska westward to the Aleutian Islands, and Murata (in Okutani, 1977) indicated that the potential fishery yield of *O. borealijaponica* may be 50,000–200,000 t in an area west of

long. 152°E and lat. 40–45°N. If a commercial fishery does develop, accurate life-history information is essential for management purposes.

The general biology and feeding ecology of *Onychoteuthis borealijaponica* have been investigated (Naito et al., 1977b; Okutani and Murata, 1983); however, little information is available on age and growth. Average growth rates have been inferred from length-frequency distributions of sequential jigging samples (Murata and Ishii, 1977). This study suggested that the lifespan for boreal clubhook squid is approximately one year; females grow faster and attain a larger size (370 mm mantle length (ML)) than males (270 mm ML). Growth estimates from driftnet studies (Kubodera et al., 1983; Kubodera, 1986) were inconclusive because length-frequency modes were impossible to detect, possibly because of protracted spawning seasons or variable individual growth rates within a population.

The accuracy and precision of cephalopod growth estimates have been greatly enhanced through the use of daily increments within statoliths (Natsukari et al., 1991). Ageing by counting statolith increments allows the estimation of size at age and may provide information on individual age and growth rates. Hatchdates can be estimated by back calculation of daily increments. Age and growth estimates derived from statolith analysis

[1] DiNardo, G. T., and W. Kwok. In review. Estimates of fish and cephalopod catch in the North Pacific high-seas driftnet fisheries, 1990–91.

have been obtained from a variety of neritic squid species (see review by Rodhouse and Hatfield, 1990a).

The objectives of this study were to 1) estimate the age and growth of *O. borealijaponica* from statolith microstructural analysis, 2) determine the periodicity of increment formation, 3) statistically compare appropriate growth models fit to the ageing data, 4) determine the distribution of back-calculated hatching dates of *O. borealijaponica* and draw inferences about spawning locations, and 5) determine the relationship between age and maturity stages.

Materials and methods

Taxonomic clarifications

At least five onychoteuthid species are found in the North Pacific: *O. borealijaponica* from subarctic waters; an undescribed species occupying the North Pacific transition zone (~29–40°N, Bigelow, unpubl. data); and three subtropical species of the *O. banksii* complex (Young and Harman, 1987). Juvenile, subadult, and adult *O. borealijaponica* (69–343 mm ML) were separated from other onychoteuthid species based on the number of tentacular hooks (n=25–29) on each club. Identification of *O. borealijaponica* paralarvae (11.5 to 35 mm ML) was based on mantle chromatophore patterns (Bigelow, unpubl. data).

Data collection

Subadults, adults During July–September 1990, *O. borealijaponica* specimens were collected on various research cruises in the North Pacific. Most squid specimens were captured by research drift net (mesh size=48–220 mm stretch mesh) in the western and central North Pacific, but squid jigs were also used to capture specimens from the central and eastern North Pacific (Fig. 1, Table 1). Squid samples were frozen (–20°C) upon capture and returned to the laboratory for analysis.

Paralarvae, juveniles From 5 to 24 August 1991, 39 tows with a modified Cobb trawl were made along meridian 179°30'W between 36°56'N and 46°00'N, and along meridian 174°30'W between 39°00'N and 45°00'N. The trawl was dual warp, with a mouth area of approximately 140 m² when fishing and a cod-end liner constructed of 3.2 mm knotless nylon delta mesh (Wyllie Echeverria et al., 1990; Lenarz et al., 1991). Thirty-one oblique night tows (0–150 m) and eight oblique day tows (0–750 m) were conducted. *O. borealijaponica* specimens from eight tows (Fig. 1, Table 1) were sorted on
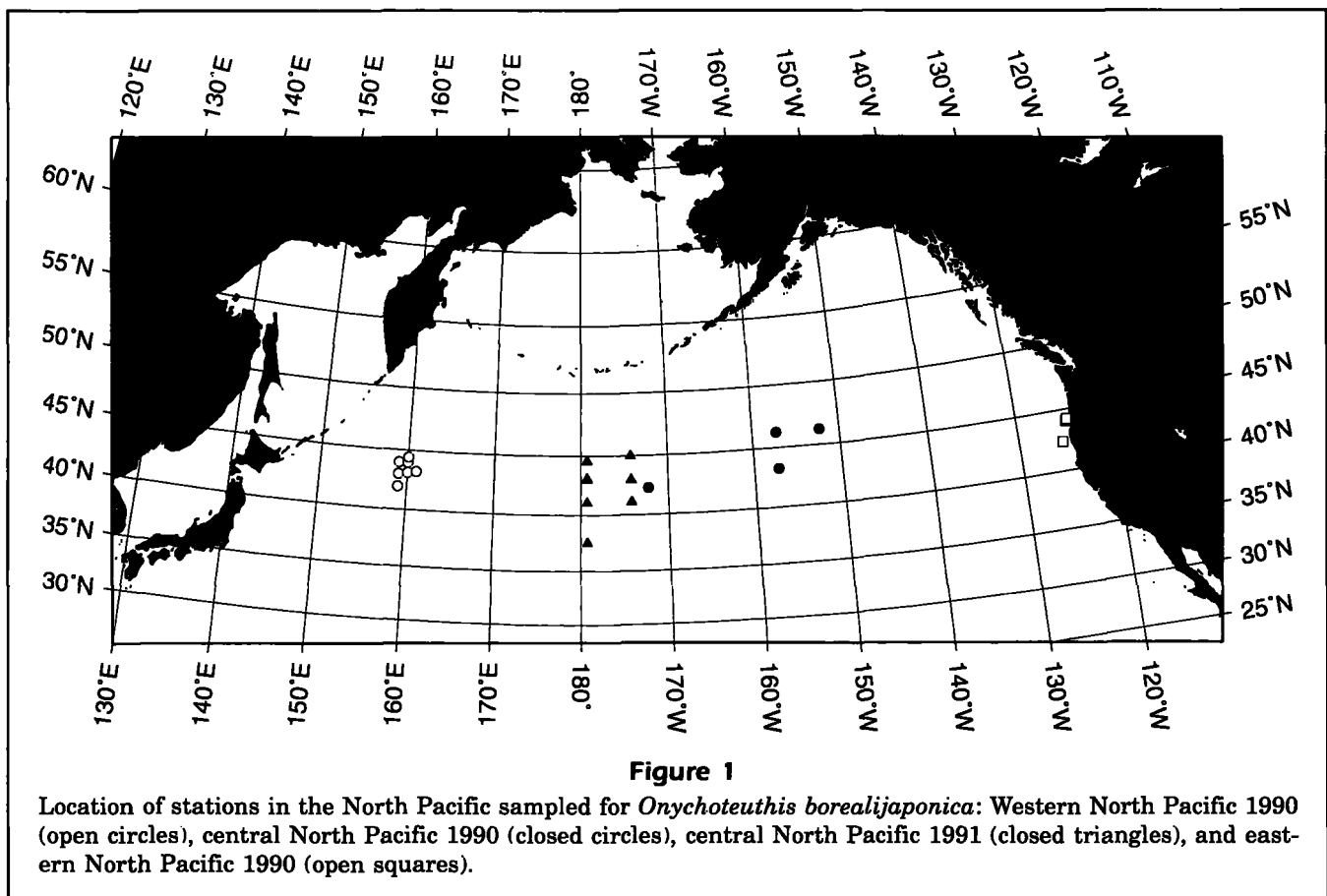
board and immediately frozen (–20°C, juveniles) or fixed in 95% ethyl alcohol (paralarvae).

Laboratory analysis

Dorsal mantle length measurements were made to the nearest millimeter (mm) on thawed specimens. Squids less than 0.5 g were blotted dry and weighed to the nearest 0.001 g, whereas larger specimens were weighed to the nearest 0.1 g. No correction was made for shrinkage of paralarvae from fixation in ethanol, because the species possesses a strong gladius and exhibited minimal shrinkage (<2%). Specimens were sexed and assigned a maturity stage (I: juvenile; II: immature; III: preparatory; IV: maturing; V: mature) based on the appearance and relative size of the gonads and accessory reproductive organs (Lipinski, 1979). Statoliths were dissected from the specimens and stored in 95% ethyl alcohol.

Statolith preparation and microstructural analysis
One statolith of the pair was mounted on a microscope slide in Eukitt resin (Calibrated Instruments Inc. 200 Saw Mill Rd., Hawthorne, NY 10532) with the concave side (anterior) facing up. The transparency of paralarval statoliths allowed their examination without further preparation (Fig. 2). The thickening of statoliths from larger squid (>35 mm ML) required that they be ground with fine-grained (1200-grade) carborundum paper and polished with 0.3–μm alumina-silica powder prior to microstructural examination.

Increments were counted beginning at the first visible increment outside the nucleus (Fig. 3A), and continued to the margin of the dorsal dome (Fig. 3B). The diameter of the circular nucleus averaged 28.0 μm (SD=2.4 μm, n=37). The precision of increment counts was assessed by using the coefficient of variation (Chang, 1982). Two nonconsecutive blind increment counts were made on each statolith with transmitted light at a magnification of 1500×. The mean of the two increment counts was accepted if the coefficient of variation was <7.0%, otherwise a third count was conducted. With this criteria, two increment counts were acceptable for 115 statoliths, whereas three increment counts were required for 11 statoliths. Hatching dates were computed by subtracting the mean increment count from the date of capture and were pooled into monthly periods. Increment counts were assumed to represent the individuals' age in days, based on the following results (periodicity of increment deposition) which provided support for the hypothesis that one increment is deposited per day.

Figure 1
Location of stations in the North Pacific sampled for *Onychoteuthis borealijaponica*: Western North Pacific 1990 (open circles), central North Pacific 1990 (closed circles), central North Pacific 1991 (closed triangles), and eastern North Pacific 1990 (open squares).

Periodicity of increment deposition Three sub-adult squid caught by jig or trawl in the central North Pacific were placed for two hours in 20 L of seawater containing 250 mg/L oxytetracycline hydrochloride (OTC). After OTC exposure, squid were maintained in a 20–L tank with flowthrough seawater under ambient photoperiod and temperature conditions. Freshly captured live saury (*Cololabis saira*) were introduced as prey, but no feeding was noted or observed. Squids survived up to 61.5 hours in captivity. Statoliths were prepared as above and illuminated with ultraviolet (Fig. 4) and natural light. Under fluorescent light, an ocular marker was aligned with the inner edge of the OTC band. The statolith was then examined under natural light, but increments peripheral to the band were difficult to count. Therefore, to determine the periodicity of increment deposition, statolith growth following OTC exposure was related to the average increment width prior to exposure. The distance from the inner edge of the OTC band to the statolith perimeter was divided by the mean width of increments prior to the OTC band. Three estimates of statolith growth after OTC exposure were made, and the average increment width calculated for 15 increments prior to the OTC band.

Statistical procedures

Mantle length-weight relationships Mantle length-weight regressions were fit to the data by using the model

$$WT(g) = a * ML(mm)^b \qquad (1)$$

Separate ML-weight equations were developed for both sexes, and a single equation was used for squid of unknown sex ($<$60 mm ML).

Fitting of size-at-age data Researchers have used a variety of different models to describe cephalopod growth (e.g., linear, logistic, von Bertalanffy), although the rationale for using a given model is usually not stated. Schnute (1981) proposed a flexible four-parameter model to describe growth which includes most growth models historically used in fisheries research as special cases. The model takes the form

$$Y(t) = \left[y_1^b + (y_2^b - y_1^b)\frac{1-e^{-a(t-t_1)}}{1-e^{-a(t_2-t_1)}} \right]^{1/b} , \qquad (2)$$

Table 1

Data on samples of *Onychoteuthis borealijaponica* collected for age analysis.

Date	Lat.	Long.	Gear	Depth (m)	Temperature (°C)	n	Mantle length (mm)
Western North Pacific							
24 Jul. 1990	42°00'N	158°58'E	Driftnet	0–10	14.9	5	197–316
25 Jul. 1990	43°03'N	158°59'E	Driftnet	0–10	15.5	12	203–311
26 Jul. 1990	44°02'N	158°56'E	Driftnet	0–10	16.1	14	214–343
28 Jul. 1990	44°00'N	160°00'E	Driftnet	0–10	16.5	15	206–339
29 Jul. 1990	43°16'N	159°58'E	Driftnet	0–10	15.7	8	204–233
06 Aug.1990	43°30'N	161°02'E	Driftnet	0–10	16.0	2	275–288
20 Sep.1990	44°45'N	160°03'E	Driftnet	0–10	15.7	1	182
					Total	57	
Central North Pacific							
SAMPLE A							
08 Jul. 1990	42°30'N	172°32'W	Driftnet	0–8.5	14.8	2	165–195
04 Aug.1990	46°30'N	152°30'W	Driftnet	0–8.5	12.1	4	147–180
10 Aug.1990	46°30'N	157°30'W	Driftnet	0–8.5	11.8	7	191–313
12 Aug.1990	43°29'N	157°27'W	Driftnet	0–8.5	14.3	1	343
SAMPLE B							
06 Aug.1991	37°59'N	179°28'W	Cobb	0–154	11.7–24.1	5	11.5–32
06 Aug.1991	37°55'N	179°26'W	Cobb	0–158	11.7–24.1	8	24–35
09 Aug.1991	41°08'N	179°30'W	Cobb	0–130	11.0–20.3	1	42
12 Aug.1991	43°12'N	179°30'W	Cobb	0–775	3.5–16.4	1	58
12 Aug.1991	43°04'N	179°30'W	Cobb	0–156	8.6–15.9	6	69–83
15 Aug.1991	44°59'N	179°27'W	Jig	0–5	12.6	7	119–190
18 Aug.1991	45°00'N	174°31'W	Cobb	0–162	6.8–13.2	4	75–82
20 Aug.1991	43°00'N	174°30'W	Cobb	0–142	8.8–16.5	2	72–78
22 Aug.1991	41°14'N	174°29'W	Cobb	0–730	5.6–21.1	1	66
					Total	49	
Eastern North Pacific							
18 Aug.1990	42°47'N	125°25'W	Jig	0–100	15.1	5	214–251
19 Aug.1990	44°12'N	124°54'W	Jig	0–100	15.9	2	229–236
04 Sep.1990	44°23'N	124°44'W	Jig	0–75	16.4	13	218–312
					Total	20	

where $Y(t)$ is the estimated length or weight at age t, and y_1 and y_2 represent size at two ages t_1 and t_2, which are typically the youngest and oldest individuals in the sample. The estimated parameters a and b describe how the model connects y_1 and y_2. Values of a and b and their 95% confidence intervals lead to the selection of other submodels.
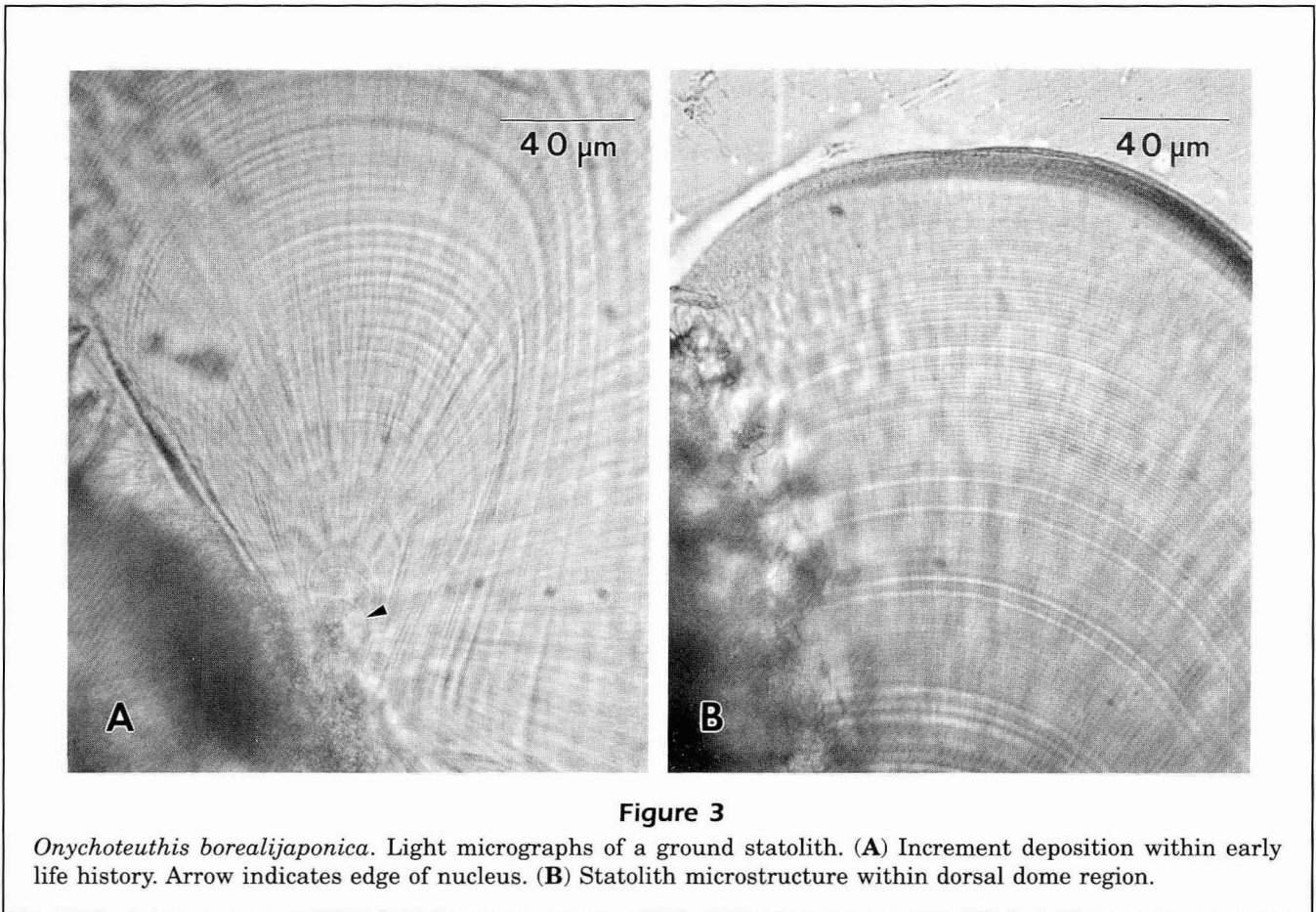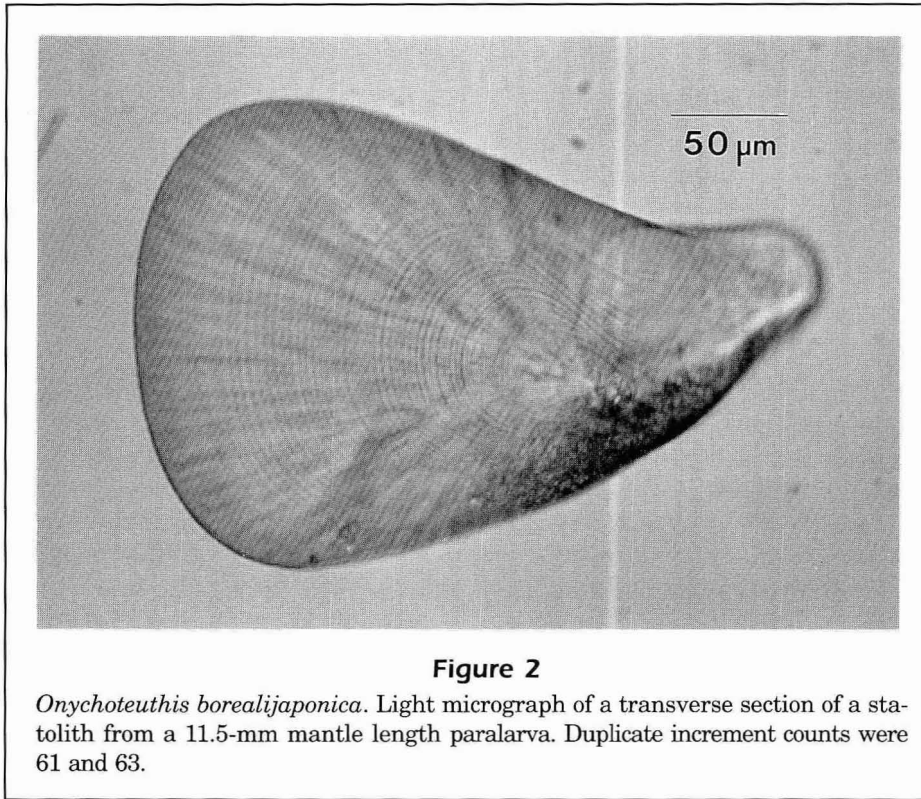
The Schnute model (written in Microsoft Quickbasic) was fit to the size-at-age data (Fig. 5) by nonlinear regression on an IBM-compatable microcomputer. Growth modelling was restricted to individuals from the central North Pacific samples, because of inadequate age representation from the western and eastern North Pacific samples. Paralarval size-at-age estimates were included in the growth models for males and females, because

size-at-age results were similar for juvenile (66–83 mm ML) males and females.

Model comparison If we assume that the Schnute model exactly predicts the size of an individual, then the residual sum of squares (*RSS*) of this full model is an estimate of measurement error. To ascertain if a reduced model with fewer parameters (e.g., 2–parameter exponential) adequately describes the data, the *RSS*'s from the reduced model and full model were compared using an F test statistic:

$$f = \frac{(RSS_R - RSS_F)/(DF_F - DF_F)}{RSS_F/DF_F}$$
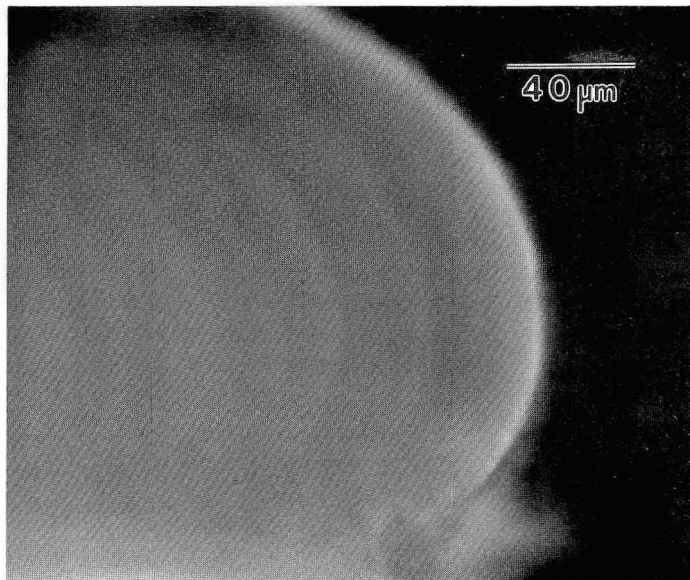
(3)

with $DF_R - DF_F, DF_F$ degrees of freedom,

Figure 2

Onychoteuthis borealijaponica. Light micrograph of a transverse section of a statolith from a 11.5-mm mantle length paralarva. Duplicate increment counts were 61 and 63.

Figure 3

Onychoteuthis borealijaponica. Light micrographs of a ground statolith. (**A**) Increment deposition within early life history. Arrow indicates edge of nucleus. (**B**) Statolith microstructure within dorsal dome region.

Figure 4

Onychoteuthis borealijaponica. UV micrograph of a ground statolith stained with tetracycline.

where RSS_F is the RSS from the full (Schnute) model, RSS_R is the RSS from the reduced (exponential) model, DF_F is the number of degrees of freedom from the full model, and DF_R is the number of degrees of freedom from the reduced model (Neter et al., 1985).

Differences in the slopes of the ML-weight and size-at-age relationships by sex and geographical location were compared with analysis of covariance (ANCOVA) and F-tests (Sokal and Rolff, 1981). Data were initially ln-transformed, and ANCOVA was used to test for differences in slopes of the linearized equations. Elevations of the linearized equations were compared with F-tests. Analyses were performed on central North Pacific male and female growth data and western North Pacific female data with the assumption that females in the western North Pacific exhibited a similar type of growth as individuals in the central North Pacific. There were too few individuals to test for differences in growth rates
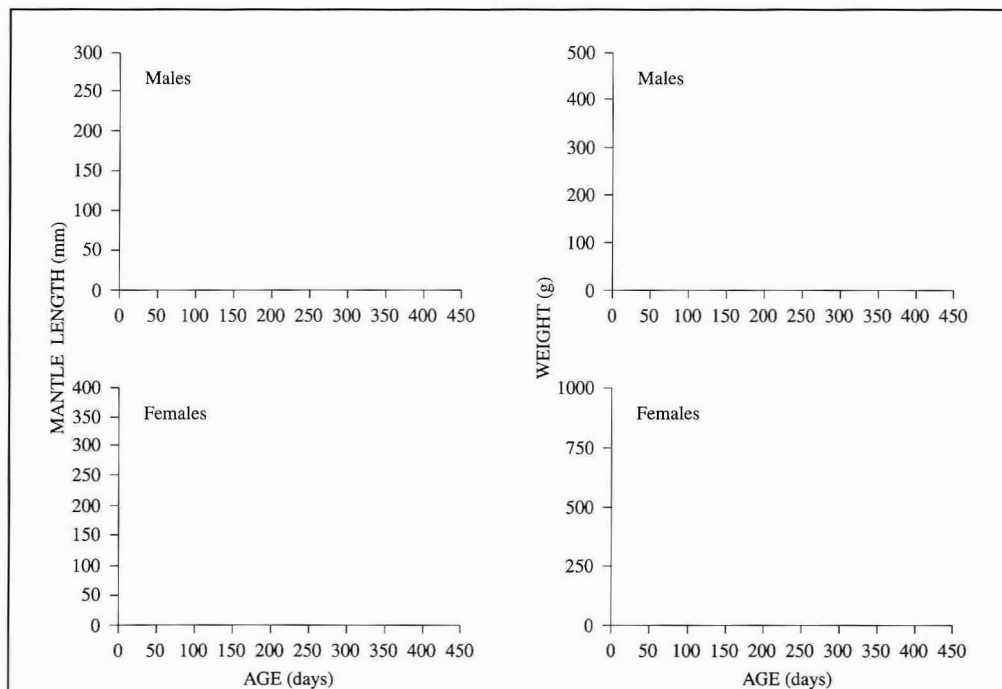

Figure 5

Relation between age (determined by number of increments within statoliths) and mantle length (mm) and weight (g) for male and female *Onychoteuthis borealijaponica*. Western North Pacific 1990 (open circles), central North Pacific 1990 (closed circles), central North Pacific 1991 (closed triangles = juveniles-subadults, open triangles = unknown sex), and eastern North Pacific 1990 (open squares).

of western North Pacific males or eastern North Pacific males and females.

Results

Statolith analysis

Statolith microstructural analysis was applied to 131 squid from the western, central, and eastern North Pacific. Five statoliths (3.8%) were broken or poorly sectioned and excluded from further analysis. The coefficient of variation about the mean for the aged samples (n=126) averaged 3.7% based on 2–3 increment counts for each statolith. No obvious trend existed in the coefficient of variation with the increment count or body size.

Periodicity of increment formation

A fluorescent OTC band was evident in the statoliths of the three squid exposed to oxytetracycline. While increments peripheral to the inner edge of the OTC band could not be reliably counted, the relation between the growth of the statolith, rearing period, and the width of increments prior to the OTC band suggested that increments were deposited daily (Table 2). Statolith growth in the dorsal dome region ranged from 1.4 to 4.3 μm over the rearing period (26–61.5 hr). The average number of increments deposited per day after oxytetracycline exposure was 1.30 (range 1.08–1.52) for the three squid.

Mantle length-weight relationships

The ML-weight relationship for paralarval *O. borealijaponica* from the central North Pacific is represented by the equation

$$WT = 2.484 \times 10^{-5} ML^{3.015}; R^2 = 0.99 (n = 36). \quad (4)$$

The ML-weight relationships for juvenile-adult *O. borealijaponica* from the western, central, and eastern North Pacific are represented by the following equations:

males:

$$WT = 1.873 \times 10^{-4} ML^{2.596}; R^2 = 0.96 (n = 43) \quad (5)$$

females:

$$WT = 3.521 \times 10^{-5} ML^{2.915}; R^2 = 0.99 (n = 68) \quad (6)$$

The slopes of the ML-weight regressions for male and female *O. borealijaponica* were significantly different ($P<0.001$).

Growth

A good relationship existed between the number of increments within statoliths and squid size for individuals in the central North Pacific (Fig. 5). An exponential model (Table 3, Equation 7) was appropriate to describe the ML-at-age relationship (f=1.82, F=2.49) for females (paralarvae-subadult) in the central North Pacific. A logistic model was appropriate to describe the ML-at-age relationship (f=1.85, F=2.93) for males (paralarvae-adult) in the central North Pacific. However, the oldest individual (394 days, 245 mm ML) was a mature male (stage V) which influenced the type of model selected. Omitting that individual resulted in the selection of an exponential model (f=2.49, F=2.55) over a logistic model (f=4.73, F=2.94) to describe paralarval-subadult growth (Table 3, Equation 8). Exponential models were also fit to weight-at-age data for paralarval-subadult males and females (Table 3, Equations 9 and 10).

Growth in length (% increase in length per day) was similar for males and females (0.80% ML/day) in the central North Pacific, while growth in weight was faster for females (1.90% WT/day) than males (1.40% WT/day). By using the exponential models, mantle length, weight-at-age, and absolute growth

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Table 2

Age validation information for *Onychoteuthis borealijaponica* with oxytetracycline (OTC) technique. Width of oxytetracycline band is the distance observed between the fluorescent band and the margin of the statolith. Mean increment width is that of the outer 15 increments formed prior to the OTC band.

No.	ML (mm)	Rearing period (hr)	Width of oxytetracycline band (μm)	Mean increment width (μm)	Estimated increments per day
1	162	26	1.4	1.19	1.08
2	166	61.5	4.3	1.10	1.52
3	175	44	2.8	1.16	1.32

Table 3

Exponential equations for growth of male and female *Onychoteuthis borealijaponica* from the central North Pacific Ocean.

Variable	Age interval (d)	n	Equation	r^2	Equation no.
Length (F)	62–376	36	$mm = 18.41e^{0.00785t}$	0.97	7
Length (M)	62–314	27	$mm = 17.17e^{0.00798t}$	0.89	8
Weight (F)	62–376	36	$g = 0.74e^{0.0188t}$	0.92	9
Weight (M)	62–314	27	$g = 2.19e^{0.0138t}$	0.82	10

rates (*AGR*, mm/day or g/day) were predicted for the initial 365 days (Table 4).

The slopes of the size-at-age regression equations for females from the western North Pacific were significantly different from those for both central North Pacific males and females (Fig. 6, Table 5). Comparisons of regression slopes between central North Pacific males and females revealed no significant differences in length or weight-at-age relationships ($P=0.424$, $P=0.307$). Testing of elevations from the central North Pacific male and female data identified a significant difference ($P<0.001$, Table 5); therefore, males and females in the central North Pacific grow in length and weight at a similar rate, but females display a significantly greater size at age than males (Table 4).

Back-calculated hatching dates

Backcalculation of hatching dates demonstrated that *O. borealijaponica* hatched in all months except March (Fig. 7). The distribution of hatching dates was not necessarily related to spawning intensity, as more subadult squid were available for age analysis than paralarvae and juveniles. Subadult and adult squid captured from July to September in the North Pacific had similar hatch dates as samples collected from the western (August–February), central (July–February), and eastern North Pacific (August–November). Paralarval and early juvenile squid captured in the central North Pacific during August 1991 were estimated to have hatched between February and June, 1991.

Maturity stage-age relationships

Maturity stages were closely related to squid size for all three sampling areas; males, however, matured at a smaller size than females (Fig. 8). Females and males recruit to the driftnet fishery after attaining maturity stages III and IV, respectively. No mature females (stage V) were captured by any sampling

Table 4

Growth of central North Pacific *Onychoteuthis borealijaponica* predicted by the exponential equations based on statolith analysis. Absolute growth rates (*AGR*) are given in mm or g per day.

Estimated age (days)	Males				Females			
	Mantle length (mm)	AGR_L	Weight (g)	AGR_W	Mantle length (mm)	AGR_L	Weight (g)	AGR_W
50	25.6	0.20	4.4	0.06	27.3	0.21	1.9	0.04
75	31.2	0.25	6.1	0.09	33.2	0.26	3.0	0.06
100	38.1	0.31	8.7	0.12	40.3	0.32	4.8	0.09
125	46.5	0.37	12.2	0.17	49.1	0.39	7.7	0.15
150	56.8	0.46	17.3	0.24	59.7	0.47	12.4	0.24
175	69.4	0.56	24.3	0.34	72.7	0.57	19.8	0.38
200	84.7	0.68	34.3	0.48	88.4	0.70	31.7	0.60
225	103.4	0.83	48.5	0.67	107.5	0.85	50.8	0.96
250	126.2	1.01	68.4	0.95	130.8	1.03	81.3	1.54
275	154.1	1.23	96.5	1.34	159.2	1.25	130.0	2.47
300	188.1	1.51	136.1	1.89	193.7	1.53	208.0	3.95
325	229.6	1.84	192.1	2.66	235.7	1.86	332.8	6.31
350	280.3	2.24	271.0	3.75	286.7	2.26	532.5	10.10
365	316.0	2.57	337.3	4.66	323.2	2.51	706.9	13.42
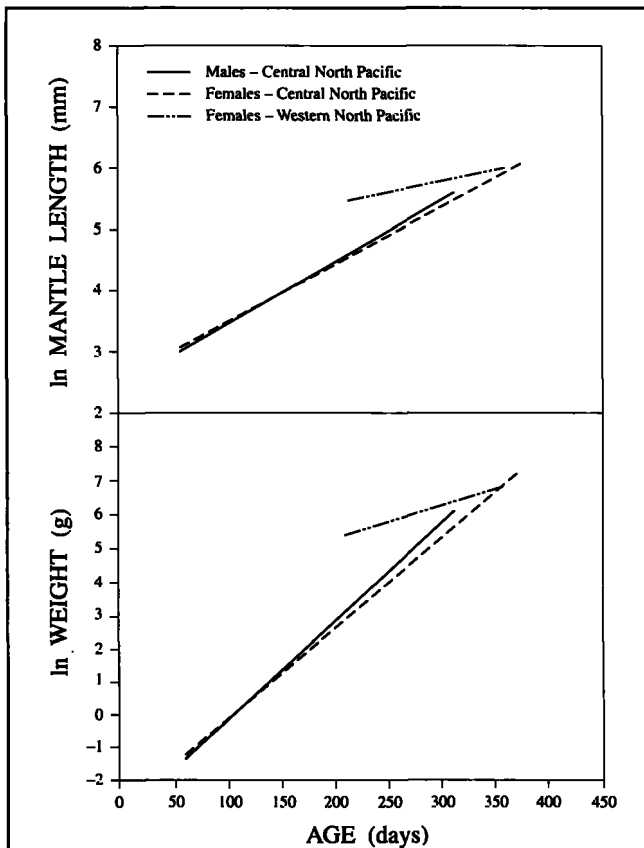
Figure 6

Log-linear growth models for male and female *Onychoteuthis borealijaponica*.

Figure 7

Estimated hatch-date distributions by month for *Onychoteuthis borealijaponica*.

method. There was some evidence that males (stage IV–V) and females (stage III–IV) in the western North Pacific were younger than similar stage individuals from the central and eastern North Pacific.

Discussion

The data presented provide support for the one-increment-deposited-per-day hypothesis within the statoliths of *Onychoteuthis borealijaponica* although further work is required to rigorously test the hypothesis. Tetracycline was incorporated into the statolith, but the animals did not feed and survival was not sufficiently long enough (2–3 days) to provide a rigorous test on the rate of increment deposition. Validation of the daily increment hypothesis has come from tetracycline labeled statolith experiments with several neritic squid species (*Illex illecebrosus*, Dawe et al., 1985, *Alloteuthis subulata*, Lipinski, 1986, *Todarodes pacificus*, Nakamura and Sakurai, 1991). Future statolith validation experiments with
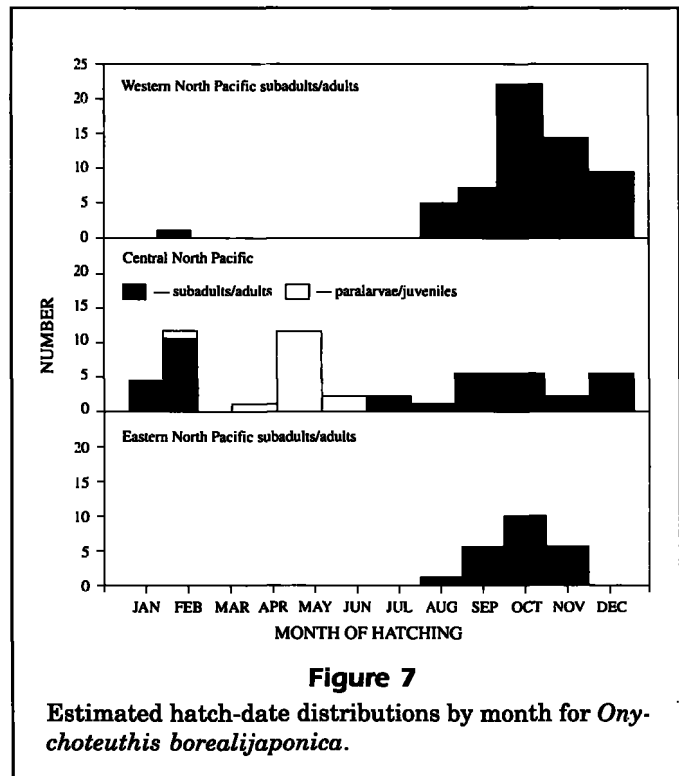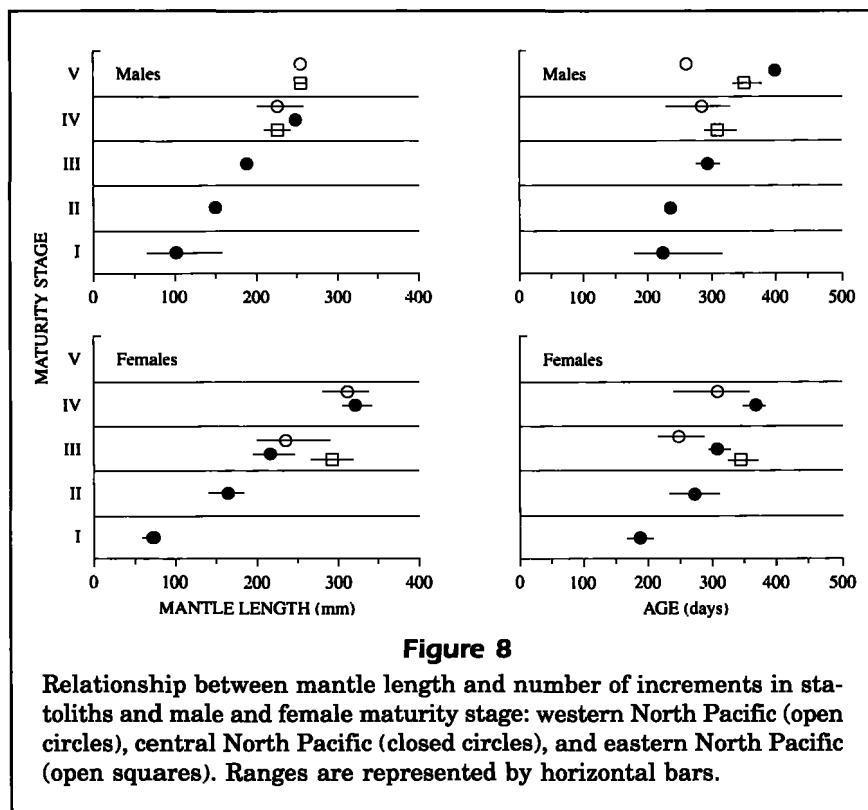
Table 5

Comparisons of *Onychoteuthis borealijaponica* growth equations based on analysis of covariance.

	Slope (F)	Elevation (F)	P
Length-at-age comparisons			
Central North Pacific, male vs. female	0.647		0.424
		1002.4	<0.001
Western North Pacific female vs. central Pacific female	62.9		<0.001
Western North Pacific female vs. central Pacific male	62.2		<0.001
Weight-at-age comparisons			
Central North Pacific, male vs. female	1.063		0.307
		1121.1	<0.001
Western North Pacific female vs. central Pacific female	65.9		<0.001
Western North Pacific female vs. central Pacific male	66.6		<0.001

Figure 8

Relationship between mantle length and number of increments in sta-
toliths and male and female maturity stage: western North Pacific (open
circles), central North Pacific (closed circles), and eastern North Pacific
(open squares). Ranges are represented by horizontal bars.

active oceanic squids (e.g., Onychoteuthidae,
Ommastrephidae) may require substantial mainte-
nance facilities to support long-term survival.

Although the rate of increment deposition derived
by the statolith marking experiment should be con-
sidered preliminary, indirect evidence was obtained
to suggest that increments were formed daily. The
hypothesis that the lifespan is 1 year (Murata and
Ishii, 1977; Naito et al., 1977b) was supported by the
present data where only 4 of the 126 individuals
aged had more than 365 increments within the sta-
tolith. In addition, back-calculated hatch dates
(July–February) of post-recruit individuals exploited
in the *O. borealijaponica* jig and *Ommastrephes
bartramii* squid driftnet fishery were consistent with
information on spawning (fall-winter) reported in
the literature (Murata et al., 1976; Murata and Ishii,
1977; Naito et al., 1977b). This study suggests that
spawning for *O. borealijaponica* occurs year round.
While subadult *O. borealijaponica* are distributed in
subarctic waters, evidence from the distribution of
paralarvae, juveniles, and sexually mature females
suggests that spawning may occur to the south of
the subarctic boundary in the North Pacific transi-
tion zone (30–42°N, terminology after Roden, 1991).
In the central and eastern North Pacific, *O.
borealijaponica* paralarvae and juveniles have been
recorded from this study (38°N, 179°30'W°) and the

coast of California (~33°N, Young,
1972), respectively. In the western
North Pacific, spawning may oc-
cur in waters of the Kuroshio Cur-
rent and Kuroshio Countercurrent
(Murata and Ishii, 1977; Naito et
al., 1977a) or between the Kuro-
shio and Oyashio fronts. Onycho-
teuthid paralarvae have been cap-
tured from both the Kuroshio Cur-
rent and Kuroshio Countercurrent
(Okutani, 1968, 1969, 1975); how-
ever, distributional evidence is in-
conclusive because of the taxo-
nomic uncertainties of the speci-
mens captured. Spawning may
occur in the transitional area be-
tween the Kuroshio and Oyashio
fronts, as sexually mature and
copulated females have been cap-
tured off Hokkaido, Japan (42°30'N,
150°40'E and 42°15'N, 144°25'E,
Murata et al., 1981).

The ML-weight relationships
obtained in this study for the
western, central, and eastern
North Pacific were similar to the
values previously given for *O. borealijaponica* cap-
tured off Japan (Murata and Ishii, 1977). Slope val-
ues obtained for the ML-weight relationships
(males=2.596, females=2.915) were similar to other
active oceanic squids having thick muscular mantle
walls. Paralarval *O. borealijaponica* had a higher
slope value (3.015) than older males and females,
consistent with previous results for loliginid squids
and benthic octopods (Forsythe and Van Heukelem,
1987).

There is no clear consensus on the type of model
which best describes cephalopod growth, although
several studies argue against the use of asymptotic
models, such as Gompertz or von Bertalanffy
(Forsythe and Van Heukelem, 1987; Saville, 1987).
Exponential models have been typically used to
describe the growth of field caught and laboratory
reared paralarval squid (Yang et al., 1986; Balch et
al., 1988; Forsythe and Hanlon, 1989; Bigelow, 1992,
1993). For growth estimates derived from statolith
analysis, a linear model is frequently used because
growth is analyzed over a short segment of the
cephalopod's life history, such as post recruitment
to a fishery (Rosenberg et al., 1980; Radtke, 1983;
Rodhouse and Hatfield, 1990b) or habitat (Jackson
and Choat, 1992).

Since the Schnute model encompasses a wide
range of growth models, it can be used to system-

atically assess the type of growth model which best describes the data. A statistical comparison of several growth models found that growth in *O. borealijaponica* from the paralarval to subadult size range could be sufficiently described with an exponential model, though there was weak evidence that a logistic model may be sufficient to describe growth in males from the paralarval to adult size range. The most appropriate growth model (exponential or logistic) for the entire life cycle of *O. borealijaponica* will emerge when sexually mature males and females are aged.

Estimated growth rates from this study were higher than estimates derived from length-frequency analysis of fisheries data (Murata and Ishii, 1977). Growth estimates based on length-frequency analysis with time often provide evidence of decreased growth rate, which is usually described by an asymptotic model (Patterson, 1988). Length-frequency analysis may be inappropriate for estimating growth in cephalopods (Jackson and Choat, 1992), either because 1) cohorts are difficult to detect because spawning occurs throughout the year, 2) variable individual growth rates produce Lee's phenomenon (Ricker, 1975), or 3) samples of a migrating population are taken at a point along the migration route, which results in overestimating growth in young squid and underestimating growth in older squid.

Growth data presented for *O. borealijaponica* from the central North Pacific provide a useful comparison of growth between males and females. The exponential models predict that males and females grow in length at similar rates (0.80% ML/day), but females grow faster in weight (1.90% WT/day) than do males (1.40% WT/day). These rates correspond closely with the average growth rates of similar sized squids from temperate waters (e.g., *Illex illecebrosus*, O'Dor, 1983; *I. argentinus*, Rodhouse and Hatfield, 1990b).

The most significant advantage of using statolith ageing techniques is the ability to produce individual rather than population statistics. Using statolith analysis, spatial variations in size at age, growth parameters, and maturity stage at age were observed between *O. borealijaponica* individuals from the western and central North Pacific. Little is known concerning genetic variation and stock structure of *O. borealijaponica* in the North Pacific; however, female squid in the western North Pacific were found to grow faster than both male and female squid in the central North Pacific and were younger at maturity stages III and IV than central North Pacific females. Apparent growth rate and maturity stage differences may be related to water

temperatures or food availability during the paralarval stage. Forsythe and Hanlon (1989) showed that temperature had a pronounced effect on the increase in length and weight of the squid *Loligo forbesi*. In their laboratory study, a temperature increase of 1°C increased the growth in length and weight of paralarval squid 0.5% and 2.0% per day, respectively. Subadults in the western Pacific may have hatched in the warm Kuroshio Current or in productive transition waters between the Kuroshio and Oyashio fronts. Paralarvae hatched in the western North Pacific may therefore experience higher temperatures or a greater abundance of prey species, or both, than paralarvae hatched in the central North Pacific, which could explain the observed spatial differences in growth.

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