Abstract.—Research was conducted to test the hypothesis that spawning of the oceanic squid *Ommastrephes bartramii* in the central North Pacific is related to the proximity of the Hawaiian Archipelago. Paralarvae were collected during five plankton surveys near the Hawaiian Island chain during the 1991–93 spawning seasons. In total, 1,720 *O. bartramii* paralarvae were collected from 406 tows. Estimation of ages and hatch dates of all squid was inferred from analysis of statolith microstructures from 85 specimens. A well-defined relationship existed between the number of statolith growth increments and the dorsal mantle length of the paralarvae. Estimated hatch dates of individuals collected during the three years surveyed ranged between mid-January and early April. Spawning sites were then estimated from hatch dates by backcalculating with physical data on the speed of ocean currents near the archipelago. Although estimated spawning of *O. bartramii* did often occur along the island chain, spawning was not limited to nearshore waters. Some animals hatched, on the basis of estimated current speeds, at least 646 kilometers away from the archipelago. Projected hatching locations of more than 72% of all collected paralarvae were at least 10 kilometers from shore. Data do not support the hypothesis that the location of the spawning grounds in this region is solely related to the position of the Hawaiian Archipelago.

Manuscript accepted 5 February 1996.
Fishery Bulletin 94:398–411 (1996).

Estimated paralarval drift and inferred hatching sites for *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) near the Hawaiian Archipelago

John R. Bower

Department of Oceanography, University of Hawaii
1000 Pope Road, Honolulu, Hawaii 96822
Present address: Research Institute of North Pacific Fisheries, Faculty of Fisheries
Hokkaido University, 3-1-1 Minato-cho, Hakodate,
Hokkaido 041, Japan

The neon flying squid, *Ommastrephes bartramii* (Lesueur), is an oceanic species occurring worldwide in subtropical and temperate waters (Roper et al., 1984). In the North Pacific, *O. bartramii* paralarvae have been collected from several areas: from January through May, paralarvae are found southeast of Honshu Island, Japan (Okutani, 1968, 1969; Saito and Kubodera, 1993); and during May, paralarvae are found along 25–26°N latitude between 143–166°E longitude, and along 29°N latitude between 161–160°E longitude (Hayase, 1995). Paralarvae also occur near the Hawaiian Archipelago from February to May (Young and Hirota, 1990; Hayase, 1995; Bower et al.[1]; Hayase[2]). A study of paralarvae collected near the Hawaiian Archipelago during 1991–93 found no systematic relationship between the distribution and abundance of *O. bartramii* paralarvae and distance from the archipelago (Bower et al.[1]). This study, however, did not account for the effects of age and paralarval drift on the distribution patterns found. The present study attempts to identify more clearly possible spawning areas by considering these factors.

Statoliths from teuthoid squids commonly contain growth increments that can be used for age determination. After conducting a detailed age analysis of *Loligo opalescens*, Spratt (1978) argued that some increments in the statolith were deposited daily, as in fish otoliths. Since then, a number of studies have been conducted to determine the frequency of increment formation (Dawe et al. [1985] on *Illex illecebrosus*; Hurley et al. [1985] on *I. illecebrosus*; Lipinski [1986] on *Alloteuthis subulata*; Jackson [1989, 1990]; and Nakamura and Sakurai [1991] on *Todarodes pacificus*; also see reviews by Rodhouse and Hatfield [1990] and Jackson [1994]). The data provide strong support for the hypothesis that growth increments form at the rate of one per day in both loliginid and ommastrephid squids. Although validation of the growth increments of *O. bartramii* has not been accomplished, I have assumed that they form daily for this study.

[1] Bower, J. R., R. E. Young, J. Hirota, P. Flament, M. Seki, and K. Bigelow. 1996. Distribution and abundance of cephalopod paralarvae near the Hawaiian Archipelago. In prep.

[2] Hayase, S. 1989. Cruise report of flying squid spawning survey by the *Hokuho Maru* in the North Pacific in April–May 1989, 21 p. Document submitted to the Annual Meeting of the International North Pacific Fisheries Commission, Seattle, Washington, 1989 October.

Vertical distribution data suggest that *O. bartramii* paralarvae occur within the 0–40 m depth layer during both day and night (Okutani, 1968; Young and Hirota, 1990). Upon hatching, paralarvae are active swimmers, but owing to their small size remain planktonic for an unknown period, presumably for several weeks. Given the role of ocean currents in the transport of cephalopod paralarvae, any analysis of cephalopod paralarval distribution requires an investigation of the prevailing oceanographic currents to determine from what region the animals have been advected since hatching. Although there are few records of naturally spawned eggs or egg masses from oceanic cephalopods and no observations of *O. bartramii* egg masses, O'Dor and Balch (1985) have suggested that pelagically spawned egg masses may become suspended in the mesopelagic zone, where reduced current speeds would limit transport of egg masses away from spawning sites. I have assumed that each paralarva hatched at the site at which it was spawned.

Korzun et al. (1979) have suggested that spawning locations of *O. bartramii* may be related to the position of islands. The present study was undertaken to determine whether and how the spawning locations of *O. bartramii* from the North Pacific are related to the proximity of the Hawaiian Archipelago. This objective was addressed by examining the distribution and ages of paralarvae captured during five plankton surveys near the Hawaiian Island chain from 1991 to 1993 with ocean current data derived from Lagrangian tracers and by estimating geostrophic flow.

Materials and methods

Collection and ageing of paralarvae

Five plankton surveys were conducted near the Hawaiian Archipelago to collect cephalopod paralarvae (Fig. 1). Plankton samples were collected during 6–15 February 1991, 5–26 February 1992, and 4–19 February 1993 with the Hokkaido University (Japan) ship FTS *Hokusei Maru*, and during 5–20 February 1991 and 22 March–7 April 1992 with the RV *Townsend Cromwell* of the National Marine Fisheries Service (NMFS). The standard sampling procedure during all surveys was to conduct 30-minute oblique tows to 100 m depth.

The *Hokusei Maru* February 1991 (*HM*-Feb 91) survey sampled paralarvae at seven stations along an inshore–offshore transect to the northeast of the Hawaiian Island chain from Kauai Island (Kauai transect), including a lone station in the lee of Hawaii Island. Windward stations were positioned 9, 16, 106, 235, 349, 460, and 583 kilometers offshore. Thirty-six tows (mean depth=95 m; SD=9 m) were taken. Sampling consisted of five back-to-back replicate tows at each station. This and subsequent *Hokusei Maru* surveys used a 4-m^2 ring net equipped with 0.505-mm mesh, a General Oceanics flowmeter, and a Benthos time-depth recorder.

The *Townsend Cromwell* February 1991 (*TC*-Feb 91) survey sampled at ten stations along the archipelago. Transects orthogonal to the archipelago were

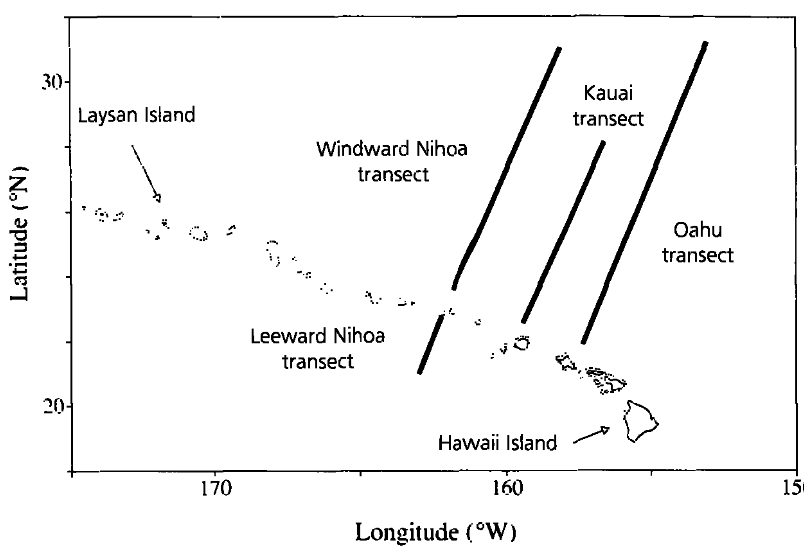

Figure 1
Map of the Hawaiian Archipelago showing the study area and transects surveyed during the five cruises.

abandoned because of inclement weather north of the ridge, restricting most sampling to nearshore waters. Stations were located 13, 14, 15, 16, 25, 28, 28, 207, 228, and 232 kilometers offshore. Forty-four tows were conducted in a stepped oblique fashion (mean depth=93 m; SD=12 m). Sampling consisted of between one and seven back-to-back replicate tows at each station with a 4-m^2 ring net equipped with 0.505-mm mesh.

During the *Hokusei Maru* February 1992 (*HM*-92) survey, paralarvae were collected along the windward Nihoa and Kauai transects, including three stations southwest of the archipelago along the leeward Nihoa transect and a lone station in the lee of Oahu Island. The Kauai transect included stations sampled during the *HM*-91 survey. One hundred thirty-one tows were collected at sixteen sampling stations (mean depth=70 m; SD=14 m). Owing to high variability in the catch rates from the *HM*-91 survey, the number of tows taken at each sampling station was increased from five to between seven and ten back-to-back replicate tows. Stations along the Kauai transect were located 11, 41, 142, 235, 337, 471, 585, and 713 kilometers offshore. Nihoa transect stations were located 26, 181, and 269 kilometers windward, and 25, 126, and 256 kilometers leeward of the archipelago. Four scheduled stations along the windward Nihoa transect were canceled because of inclement weather.

During the RV *Townsend Cromwell* March–April 1992 (*TC*-92) survey, four to eight replicate tows were conducted at fourteen stations along the windward Nihoa and Oahu transects. One hundred tows (96 with a 2-m^2 ring; 4 with a 4-m^2 ring) were conducted in a stepped oblique fashion (mean depth=94 m; SD=13 m). The net carried a Wildlife Computers time-depth recorder. Stations were located between 52 and 1,161 kilometers offshore.

During the *Hokusei Maru* February 1993 (*HM*-93) survey, paralarvae were collected along the same two transects, northeast of the Hawaiian Island chain, that had been sampled in February 1992, including three stations southwest of the archipelago (leeward Nihoa transect) and a lone nearshore test station (only two tows conducted) northeast of Oahu Island. Ninety-five tows (mean depth=92 m; SD=23 m) were collected at twelve sampling stations. Seven to ten back-to-back replicate tows were taken at each station.

Specimens from the *Hokusei Maru* surveys were fixed in 4% formalin and preserved in 50% isopropyl alcohol within 3–6 hours to prevent possible acidic degradation of the calcareous statoliths. *TC*-91 survey samples were fixed in 10% formalin and preserved in 50% isopropyl alcohol. *TC*-92 survey samples were fixed in 6% formalin and preserved in 50% isopropyl alcohol. Statoliths from specimens stored in formalin longer than six hours darkened and proved unreadable.

Paralarvae of the family Ommastrephidae were identified to genus and species level according to figures and descriptions of Hawaiian ommastrephids published by Young and Hirota (1990) and Harman and Young (1985). The dorsal mantle length of each *O. bartramii* paralarva was measured to the nearest 0.1 mm with an ocular micrometer in a stereomicroscope.

Statoliths were removed from the paralarvae with fine dissecting forceps under a stereomicroscope. First, the paralarval funnel was removed, revealing the ovate statocyst. Statoliths were clearly visible within the statocyst as paired, white, opaque structures. The excised statocyst was transferred to a microslide, where it was gently pulled apart, permitting one of the statoliths to fall onto the slide. The statocyst with the remaining statolith inside was then transferred to a separate slide where the statolith was similarly removed. Statoliths were rinsed in distilled water and air-dried before analysis. When dried, statoliths were embedded in thermal plastic by heating the plastic to 77°C.

Statoliths from 85 animals (mantle length: 1.0–4.7 mm) were used for growth increment analysis. Paralarvae used for statolith examination were collected during the *HM*-91, *HM*-92, and *TC*-92 surveys. Growth increments on *O. bartramii* statoliths consisted of two components, a broad, translucent ring and a narrow, dark ring. Using a Zeiss compound microscope (400×), increments were counted from the nucleus to the outer margin of the dorsal end of the lateral dome. Examinations were made with transmitted light. Counts of each statolith were conducted on three separate occasions and averaged for a mean increment value. Increments in the outermost portion of the lateral dome and the innermost portion near the nucleus could not be counted in some cases; therefore the number of increments on those portions was estimated by extrapolation.

Data treatment

Age for each of the 85 paralarvae used for growth increment analysis was determined from the mean of the three counts of statolith growth increments. The exponential equation $y=ae^{bx}$ was fitted to the data for the mantle-length–increment-count relationship. Age estimates of all other paralarvae were based on this relationship curve.

Estimated ocean current speeds and directions

Patterns of ocean currents near the Hawaiian Archipelago were defined by the trajectories of near-surface drifters and by dynamic height measurements from conductivity-temperature-depth (CTD) probes. Four ARGOS-tracked drifters released by the National Marine Fisheries Service were used as Lagrangian tracers of the surface currents during the 1992 survey periods to assess "typical" current speeds and directions near the Hawaiian Archipelago. Drifter positions were recorded every six hours over the survey period. Each drifter's Lagrangian net path was plotted. Geostrophic flow measurements were calculated between each pair of successive sampling stations during the three *Hokusei Maru* surveys on the basis of dynamic height measurements taken at each sampling station from CTD casts to 1,200 m. Sampling stations averaged approximately 110 km and 24 hours apart.

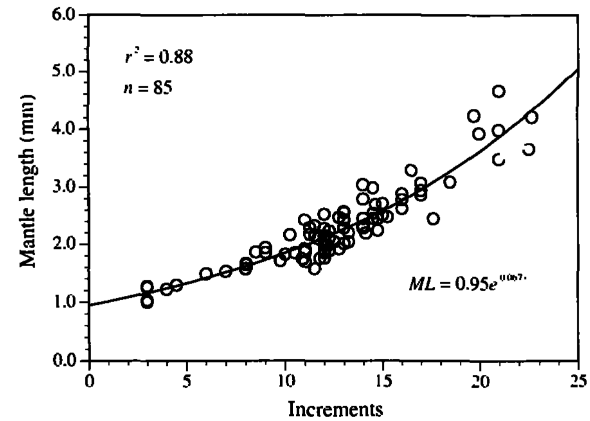

Figure 2

Relationship between paralarval mantle length and number of daily growth increments in statoliths of *Ommastrephes bartramii*, and proposed growth curve.

Results

A total of 1,720 *O. bartramii* paralarvae was collected at 41 of the 59 sampling stations, making up 16.5% of the cephalopod paralarvae caught. Sizes of *O. bartramii* ranged from 0.9 mm to 8.3 mm ML.

Age–mantle-length relationship

Statolith growth increment counts ranged from 3 to 22.7 (Table 1). A well-defined relationship existed between the number of statolith growth increments and the dorsal mantle length of the paralarvae, with the exponential function yielding a good fit for the regression (r^2=0.88) of the number of increments on the dorsal mantle length (Fig. 2). The following exponential model was fitted to the data:

$$ML = 0.95e^{(0.067x)},$$

where *ML* is the dorsal mantle length in millimeters and *x* equals the number of increments. This equation was used to estimate the ages (*x*) of the 1,635 paralarvae not examined during statolith increment analysis. The *y*-intercept of the exponential function (*a*=0.95 mm) is close to the actual hatching length (ca. 1 mm).

Size structure, ages, and projected hatch dates

The dorsal mantle length ranges of *O. bartramii* paralarvae varied slightly among surveys (Fig. 3). The largest range of size occurred during the *TC*-91 survey (0.9–8.3 mm), and the smallest range of size occurred during the *HM*-91 survey (1.0–5.6 mm).

Estimates of paralarval ages for total samples, predicted from the exponential mantle length on age model, ranged from 1 to 30 days. Projected paralarvae hatch dates for the five surveys are summarized in Figure 4. During the *HM*-91 and *TC*-91 surveys, captured paralarvae were estimated to have hatched between 13 January and 8 February. During the *HM*-92 and *TC*-92 surveys, estimated hatch dates of captured paralarvae fell between 22 January and 1 April. During the *HM*-93 survey, estimated hatch dates of captured paralarvae fell between 11 January and 6 February.

Paralarval size with distance offshore

Mean mantle lengths at each station were compared with distance from the archipelago (Fig. 5). The mean mantle lengths at each station were not significantly correlated (P>0.05; Student's t-test) with distance offshore for any of the five surveys.

Hydrographic observations

No clear advective current patterns could be estimated from the ARGOS-tracked drifters' tracks (Fig. 6). Average net displacement of the four drifters near the Hawaiian Archipelago was 2.5 km per day. During the *HM*-91 survey, CTD data revealed surface to 50-m flows ranging from 4.1 to 16.0 cm per second relative to 1,000 m in reversing bands relative to the archipelago north of the island chain. During the *HM*-92 survey, CTD data revealed flows ranging from 0.0 to 13.8 cm per second relative to 1,000 m in reversing bands relative to the archipelago both north and south of the island chain; *HM*-93 CTD data revealed flows ranging from 1.6 to 23.6 cm per second relative to 1,000 m in reversing bands both north and south of the island chain.

In summary, mean current speeds near the Hawaiian Archipelago range between 0.30 and 0.42 knots for geostrophic flow normal to the transects and about 0.06 knots for ARGOS-drifter–measured displacement, with flow near the islands complex and highly variable. The drifter data are considered to be the more reliable estimate of mean-surface drift.

Projected spawning grounds

An average current speed (2.5 km per day) estimated from the four drifters tracked in the region was used together with age estimates to infer possible areas of spawning for *O. bartramii*. To determine whether paralarvae captured at some distance from the archipelago could have been carried to their position by currents from a spawning site next to the archipelago, a "best-case" scenario was used that assumed

Table 1

Size frequency of *Ommastrephes bartramii* paralarvae for 85 statoliths examined with statolith mean increment count, standard deviation (SD), and increment count range for each dorsal mantle length (DML). Specimens were collected from *Hokusei Maru* February 1991, *Hokusei Maru* February 1992, and *Townsend Cromwell* March–April 1992 surveys.

				Count range		
DML (mm)	*n*	Count mean	SD	min	max	range
1.0	2	3.0	0.0	3.0	3.0	0
1.1	0					
1.2	1	4.0	—	—	—	—
1.3	3	3.5	0.9	3.0	4.5	1.5
1.4	0					
1.5	2	6.5	0.7	6.0	7.0	1.0
1.6	4	8.9	1.8	8.0	11.5	3.5
1.7	4	9.9	1.4	8.0	11.0	3.0
1.8	4	11.1	1.0	10.0	12.0	2.0
1.9	9	10.8	1.6	8.5	12.8	4.3
2.0	5	12.6	0.5	12.0	13.3	1.3
2.1	4	11.9	0.3	11.5	12.3	0.8
2.2	7	12.5	1.6	10.3	14.8	4.5
2.3	6	12.6	1.2	11.3	14.0	2.7
2.4	7	14.0	2.0	11	17.6	6.6
2.5	5	13.9	1.4	12	15.3	3.3
2.6	3	14.0	1.7	13	16	3.0
2.7	2	14.8	0.3	14.6	15	0.4
2.8	2	15.0	1.4	14	16	2.0
2.9	3	16.7	0.6	16	17	1.0
3.0	2	14.3	0.4	14	14.5	0.5
3.1	2	17.8	1.1	17	18.5	1.5
3.2	0					
3.3	1	16.5	—	—	—	—
3.4	0					
3.5	1	21.0	—	—	—	—
3.6	0					
3.7	1	22.5	—	—	—	—
3.8	0					
3.9	1	20.0	—	—	—	—
4.0	1	21.0	—	—	—	—
4.1	0					
4.2	2	21.2	2.1	19.8	22.7	2.9
4.3	0					
4.4	0					
4.5	0					
4.6	0					
4.7	1	21.0	—	—	—	—
Total	85					

a unidirectional flow away from the islands. Table 2 shows the estimated percentage of paralarvae taken at each sampling station that could not have been spawned within 10 km of the archipelago. The projected spawning grounds of individuals collected during the five surveys are shown in Figures 7–11.

Discussion

New information was obtained on the estimated spawning areas of the squid *Ommastrephes bartramii* with respect to the Hawaiian Archipelago over the 1991–93 winter spawning seasons. The objective of the study was to determine whether a spatial relationship exists between the Hawaiian Archipelago and *O. bartramii* spawning grounds. The results presented here suggest that although estimated spawning of *O. bartramii* did often occur along the island chain, spawning was not limited to nearshore waters; on the basis of estimated current speeds, some animals hatched at least 646 kilometers away from the archipelago. For a minimum of 72% of all paralarvae from the five surveys, projected hatching sites were located at least 10 kilometers from shore.

Statolith analysis is the most effective method for estimating age in many natural squid populations, yet preparing statoliths for counting growth increments is time-consuming, and frequently increments prove unreadable. This study showed that when a sample size is large, analysis of paralarval mantle lengths measured from a representative subsample can be used as an alternate, easier, and faster method

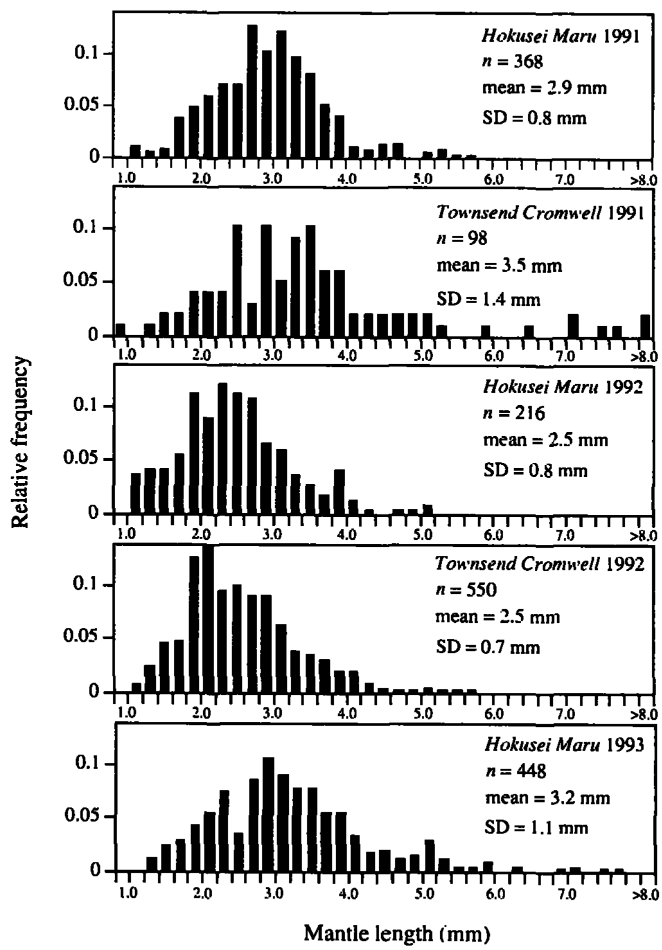

Figure 3

Size-frequency distribution of *Ommastrephes bartramii* paralarvae captured during each cruise.

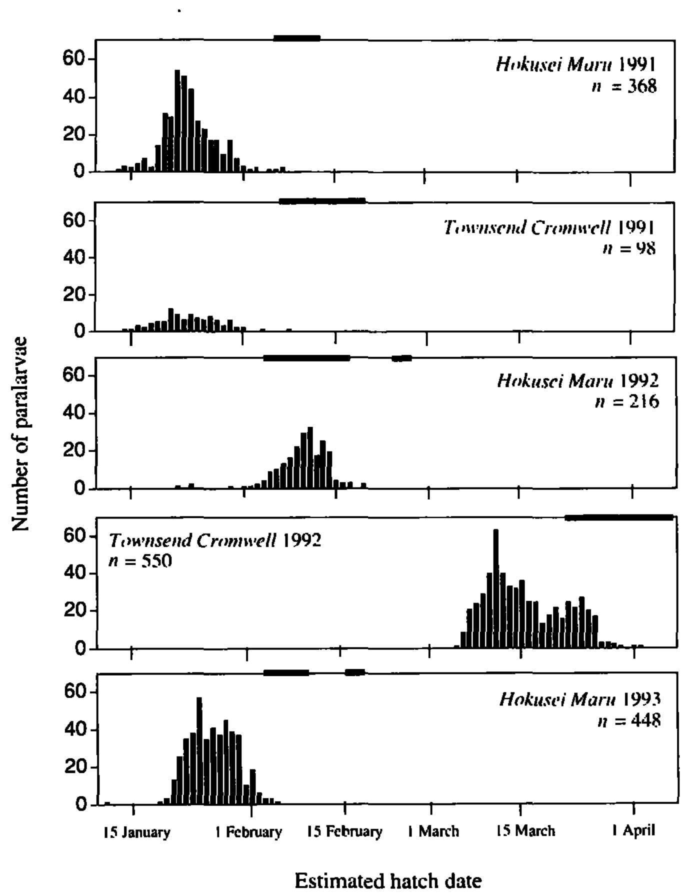

Figure 4

Frequency of projected hatch dates for *Ommastrephes bartramii* paralarvae captured during five surveys. Horizontal bars represent sampling dates.

to obtain good estimates of ages and hatch dates of *O. bartramii* paralarvae.

Growth in mantle length of *O. bartramii* paralarvae was characterized as exponential for at least 23 days after hatching. This observation agrees with that of Bigelow and Landgraf (1993), who found that growth in length of this species is exponential for at least 35 days posthatching. The growth rates of other posthatching ommastrephids have also been shown to be exponential (*Illex* sp., Balch et al., 1988; *Illex argentinus*, Arkhipkin, 1989; *Stenoteuthis oualaniensis*, Bigelow, 1991). Because growth in ommastrephids during later life tends to be linear or nearly linear, these data suggest that the overall form of growth may be approximately described as sigmoidal.

Estimated hatch dates of individuals collected during the three years surveyed ranged between mid-January and early April. Young and Hirota (1990) estimated that paralarvae caught in 1986 were spawned between late February and early April. As noted by Young and Hirota (1990), spawning may occur over a longer period, but synoptic surveys were conducted only between February and April. Surface plankton tows, conducted while the vessel drifted, and nighttime jigging at a sampling station 100 kilometers north of Oahu during March 1992, June 1992, December 1992, and April 1993, caught neither adult nor paralarval *O. bartramii* (Bower, personal observ.). More extensive nighttime jigging off the northeast coast of Oahu during mid-September–early October 1992 failed to capture adult *O. bartramii* (Bower, personal observ.). Harman and Young (1985) failed to catch *O. bartramii* paralarvae off leeward Oahu during December 1983, April 1984, August 1984, and October 1984.

Paralarvae captured over the five surveys showed a fairly broad size range of about 1–8 mm mantle length at each station, suggesting several possible spawning scenarios. If spawning were isolated to specific geographical areas, synoptic sampling would pick up different size ranges of paralarvae, depending on the proximity of the sampling site to the spawning site. Consistently large size ranges suggest that spawning is not spatially isolated. Furthermore, they suggest that spawning by the local population does not occur in intermittent bursts but is occurring over an extended period. Estimated hatch dates confirm this. The largest squid caught was 8.3 mm, suggesting that this is approximately the size at which paralarvae are fully capable of avoiding the 4-m^2 plankton trawl or that they leave the upper 100

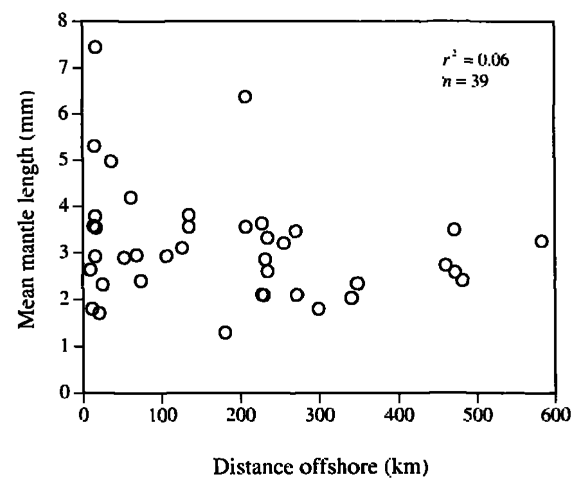

Figure 5

Relationship between mean mantle length of *Ommastrephes bartramii* paralarvae collected from each station and distance of station from land. Data from all five cruises are combined. Correlation is not significant ($P>0.05$; Student's t-test).

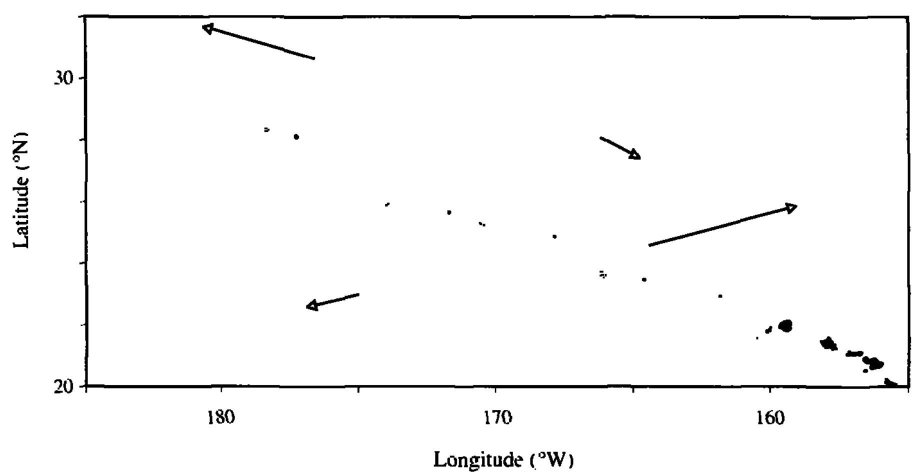

Figure 6

Net distance traveled by four ARGOS-tracked drifters near the Hawaiian Archipelago during the 1992 *Hokusei Maru and Townsend Cromwell* cruises. Time period: 22 January–1 April 1992.

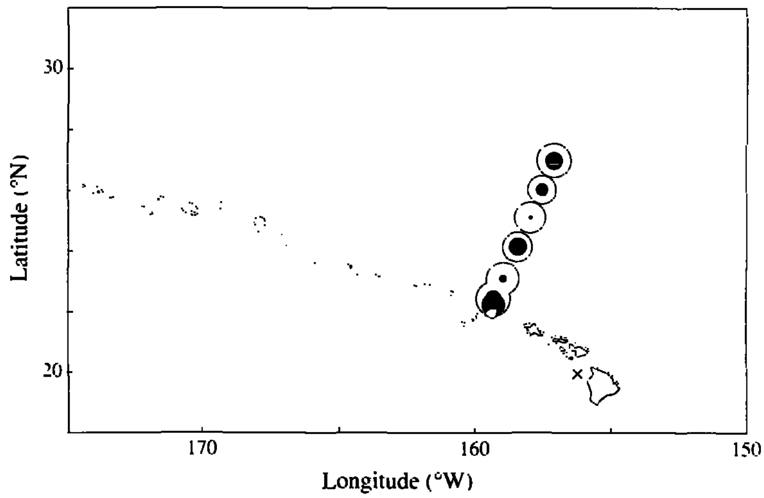

Figure 7

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1991 *Hokusei Maru* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. × = station with no *O. bartramii* paralarvae present.

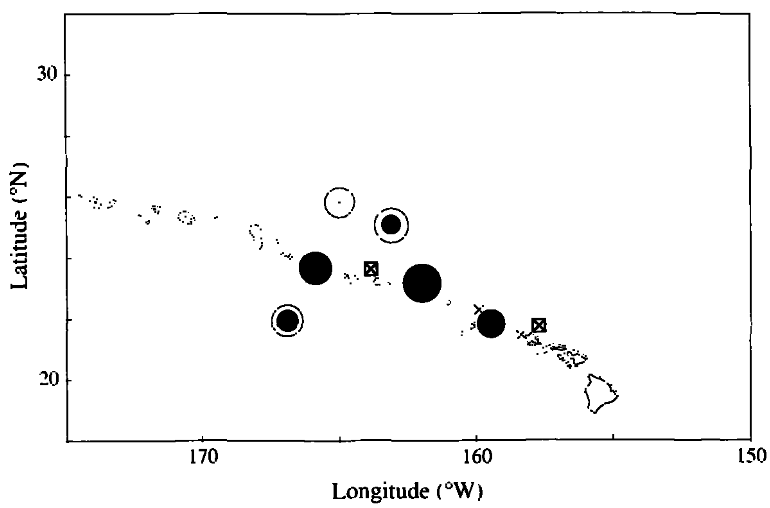

Figure 8

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1991 *Townsend Cromwell* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. ⊠ = station with one *O. bartramii* paralarva present but no mantle length measurement recorded. × = station with no *O. bartramii* paralarvae present.

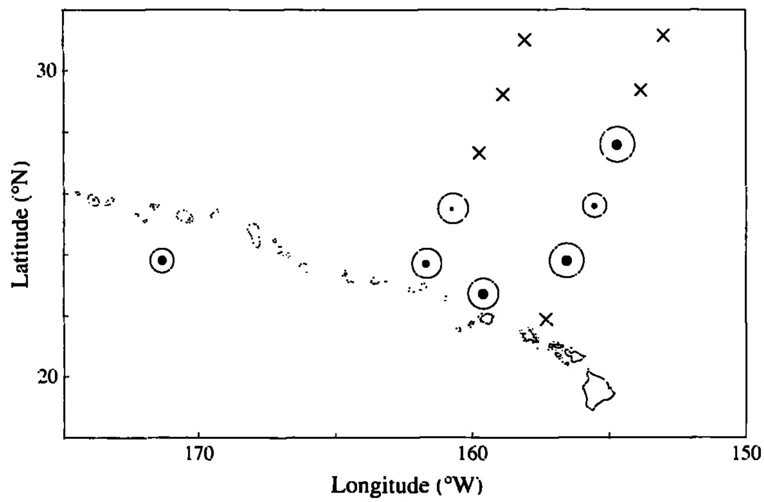

Figure 9

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1992 *Hokusei Maru* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. x = station with no *O. bartramii* paralarvae present.

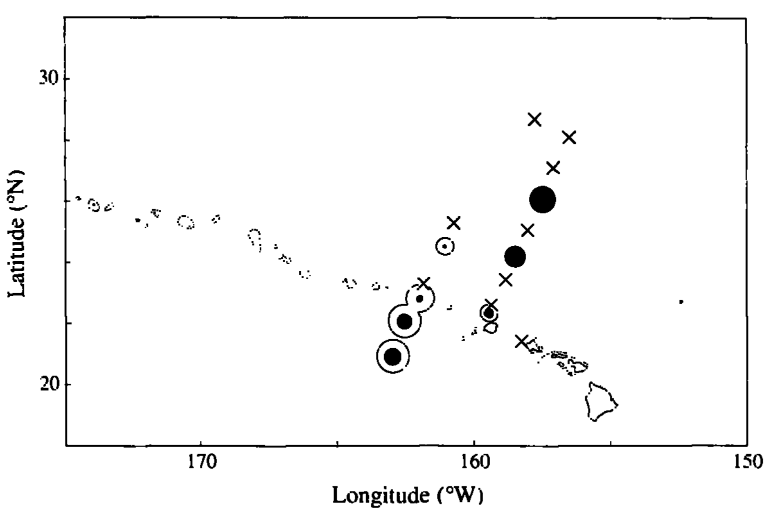

Figure 10

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1992 *Townsend Cromwell* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. x = station with no *O. bartramii* paralarvae present.

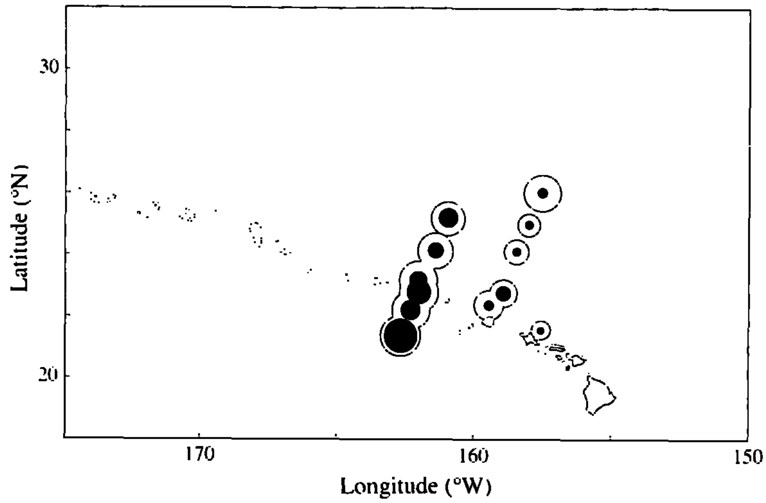

Figure 11

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1993 *Hokusei Maru* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station.

Table 2

Estimated hatching localities of *O. bartramii* paralarvae relative to the Hawaiian Archipelago (assuming a unidirectional flow away from the archipelago). Stn = station number; DO = station distance from archipelago; Catch = number captured; Min age = age of youngest paralarvae; Max age = age of oldest paralarvae; Max distance traveled = maximum distance the oldest paralarvae could have traveled after hatching; and Minimum distance from land = the closest to the archipelago the largest paralarvae could have hatched. *XX* = indicates spawning of largest animal could have occurred at archipelago. % = percentage of paralarvae of all ages from each station that would have hatched ≥10 km from the archipelago. Cruise total = percentage of paralarvae of all ages from entire survey that must have hatched ≥10 km from the archipelago. Total samples = percentage of paralarvae of all ages from all surveys combined that must have hatched ≥10 km from the archipelago. NC = no increment count.

Stn.	DO (km)	Catch (no.)	Min age (d)	Max age (d)	Max distance traveled (km)	Minimum distance from land (km)	%
***Hokusei Maru* February 1991 survey**							
1	9	2	14.8	14.8	40	*XX*	0
2	16	26	10.7	24.9	62	*XX*	0
3	106	168	4.6	23.7	59	47	100
4	235	56	12.0	21.1	53	182	100
5	349	43	2.2	22.6	56	293	100
6	460	57	8.4	20.5	51	409	100
7	583	16	12.0	24.7	62	521	100
8	33	0	—	—	—	—	—
Cruise total							92
***Townsend Cromwell* February 1991 survey**							
1	228	4	14.8	22.6	56	172	100
2	15	2	22.9	25.6	64	*XX*	0
3	232	59	0.8	21.7	54	178	100
4	207	28	13.2	24.4	61	146	100
5	28	1	NC	NC	—	—	—
6	16	4	26.9	30.1	75	*XX*	0
7	28	0	—	—	—	—	—
8	13	1	19.8	19.8	49	*XX*	0
9	25	1	NC	NC	—	—	—
10	14	0	—	—	—	—	—
Cruise total							93

meters during the day. If spawning was limited to waters near the island chain, a gradient in size with distance from shore would be expected. Presumably smaller animals would be caught nearshore and larger animals farther offshore. No correlation was found between size and distance from shore.

Drifter data confirm the picture of circulation near the Hawaiian Archipelago that flows are complex and highly variable throughout the islands. Although speeds of four drifters were averaged to estimate a general flow speed in the region, determining where particular paralarvae originated could best be deter-

Table 2 (continued)

Stn.	DO (km)	Catch (no.)	Min age (d)	Max age (d)	Max distance traveled (km)	Minimum distance from land (km)	%
***Hokusei Maru* February 1992 survey**							
1	14	0	—	—	—	—	—
2	11	2	6.6	12.6	31	*XX*	0
3	41	0	—	—	—	—	—
4	142	0	—	—	—	—	—
5	235	1	14.8	14.8	37	198	100
6	337	0	—	—	—	—	—
7	471	1	18.7	18.7	47	424	100
8	585	0	—	—	—	—	—
9	713	0	—	—	—	—	—
10	732	0	—	—	—	—	—
11	269	0	—	—	—	—	—
12	181	23	2.2	12.0	30	151	100
13	26	0	—	—	—	—	—
14	25	129	4.6	20.5	51	*XX*	2
15	126	49	10.7	23.7	59	67	100
16	256	37	12.0	23.7	59	197	100
Cruise total							44
***Townsend Cromwell* March–April 1992 survey**							
1	228	65	5.7	17.1	43	185	100
2	52	195	6.6	22.0	55	*XX*	54
3	74	103	4.6	21.1	53	21	100
4	299	38	2.2	22.0	55	244	100
5	526	0	—	—	—	—	—
6	759	0	—	—	—	—	—
7	972	0	—	—	—	—	—
8	1161	0	—	—	—	—	—
9	954	0	—	—	—	—	—
10	709	145	6.6	25.1	63	646	100
11	482	2	3.5	17.1	43	439	100
12	272	8	6.6	24.4	61	211	100
13	61	0	—	—	—	—	—
Cruise total							84
***Hokusei Maru* February 1993 survey**							
1	20	12	4.6	13.2	33	*XX*	0
2	472	6	6.6	26.6	66	406	100
3	341	16	5.7	16.2	40	301	100
4	230	43	5.7	17.5	44	186	100
5	68	20	10.0	19.8	49	19	100
6	15	137	6.6	21.4	53	*XX*	0
7	271	69	13.2	24.4	61	210	100
8	135	18	10.7	25.6	64	71	100
9	15	63	12.0	27.8	69	*XX*	0
10	36	15	16.7	28.6	71	*XX*	0
11	135	53	13.7	27.6	69	66	100
12	207	2	23.7	29.1	73	134	100
Cruise total							51
Total samples							72

mined by sampling near a drifter that had been tracked. Dynamic height variations reveal information about the longitudinal extent of the reversing flows along the Hawaiian Ridge. Measurements from CTD probes support the findings of studies that suggest the existence of bands of fairly strong currents that are immediately adjacent to the windward side of the Hawaiian Ridge and that are flowing in opposite directions (White, 1983; Mysak and Magaard, 1983).

Bower et al.[1] suggested that distribution of *O. bartramii* paralarvae is not related to the position of the Hawaiian Archipelago. The results presented here confirm this and indicate that most paralarvae captured during the five surveys were hatched at least 10 kilometers from shore, so that spawning occurs predominantly in oceanic waters.

Acknowledgments

I am grateful to Richard E. Young, Jed Hirota, Pierre Flament, and Stewart Reid for their guidance and assistance during this study. I thank Michael Seki for providing specimens and staff of NMFS for providing drifter data. I appreciate reviews of this paper by Earl Dawe, Paul Rodhouse, Marek Lipinski, Roger Villanueva, George Jackson, and two anonymous reviewers. Support for this study was provided by Hawaii Sea Grant under grant number NA89AA-D-SG063 awarded to R. E. Young. Additional support was provided by a grant from the East-West Center. This work is part of a Master's thesis submitted to the Department of Oceanography, University of Hawaii, December 1994. Research was conducted as part of a 5-year cooperative fisheries program between the University of Hawaii, Department of Oceanography, and Hokkaido University (Japan), Faculty of Fisheries.

Literature cited

Arkhipkin, A. I.
1989. Edad y crecimiento del calamar (*Illex argentinus*). Frente Maritimo 6(A):25–35.

Balch, N., A. Sirois, and G. V. Hurley.
1988. Growth increments in statoliths from paralarvae of the ommastrephid squid *Illex* (Cephalopoda: Teuthoidea). Malacologia 29:103–112.

Bigelow, K. A.
1991. Age and growth of three species of squid paralarvae from Hawaiian waters, as determined by statolith microstructures. M.Sc. thesis, Univ. Hawaii, Honolulu, HI, 78 p.

Bigelow, K. A., and K. C. Landgraf.
1993. Hatch dates and growth of *Ommastrephes bartramii* paralarvae from Hawaiian waters as determined from statolith analysis. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fisheries biology, p. 15–24. Tokai Univ. Press, Tokyo, Japan.

Dawe, E. G., R. K. O'Dor, P. H. Odense, and G. V. Hurley.
1985. Validation and application of an ageing technique for short-finned squid (*Illex illecebrosus*). J. Northwest Atl. Fish. Sci. 6:101–116.

Harman, R. F., and R. E. Young.
1985. The larvae of ommastrephid squids (Cephalopoda, Teuthoidea) from Hawaiian waters. Vie Milieu 35:211–222.

Hayase, S.
1995. Distribution of spawning grounds of flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean. Jpn. Agric. Res. Quart. 29(1):65–72.

Hurley, G. V., P. H. Odense, R. K. O'Dor, and E. G. Dawe.
1985. Strontium labeling for verifying daily growth increments in the statolith of the short-finned squid (*Illex illecebrosus*). Can. J. Fish. Aquat. Sci. 42:380–383.

Jackson, G. D.
1989. The use of statolith microstructures to analyze life-history events in the small tropical cephalopod, *Idiosepius pygmaeus*. Fish. Bull. 87:265–272.
1990. Age and growth of the tropical near-shore loliginid squid *Sepioteuthis lessoniana* determined from statolith growth ring analysis. Fish. Bull. 88:113–118.
1994. Application and future potential of statolith increment analysis in squids and sepioids. Can. J. Fish. Aquat. Sci. 51:2612–2625.

Korzun, Yu. V., K. N. Nesis, Ch. M. Nigmatullin, A. A. Ostapenko, and M. A. Pinchukov.
1979. New data on the distribution of squids, family Ommastrephidae, in the World Ocean. Okeanologiya 19(4):729–733.

Lipinski, M. R.
1986. Methods for the validation of squid age from statoliths. J. Mar. Biol. Assoc. (U.K.) 66:505–526.

Mysak, L. A., and L. Magaard.
1983. Rossby wave driven Eulerian mean flows along nonzonal barriers, with applications to the Hawaiian Ridge. J. Phys. Oceanogr. 13:1716–1725.

Nakamura, Y., and Y. Sakurai.
1991. Validation of daily growth increments in statoliths of Japanese common squid *Todarodes pacificus*. Nippon Suisan Gakkaishi. 57(1):2007–2011.

O'Dor, R. K., and N. Balch.
1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. Northwest Atl. Fish. Organ. Sci. Counc. Stud. 9:69–76.

Okutani, T.
1968. Studies of early life history of decapoden Mollusca—III. Bull. Tokai Reg. Fish. Res. Lab. 41:23–29.
1969. Studies on early life history of decapoden Mollusca—IV. Bull. Tokai Reg. Fish. Res. Lab. 55:9–57.

Rodhouse, P. G., and E. M. C. Hatfield.
1990. Age determination in squid using statolith growth increment. Fish. Res. 8:323–334.

Roper, C. F. E., M. J. Sweeney, and C. E. Nauen.
1984. FAO species catalogue: an annotated and illustrated catalogue of species of interest to fisheries. Vol. 3: Cephalopods of the world. FAO Fish. Synop. 125, 277 p.

Saito, H., and T. Kubodera.
1993. Distribution of ommastrephid rhynchoteuthion paralarvae (Mollusca: Cephalopoda) in the Kuroshio Region. *In* Recent advances in cephalopod fisheries biology, p. 457–466. Tokai Univ. Press, Tokyo, Japan.

Spratt, J. D.
1978. Age and growth of the market squid, *Loligo opalescens* Berry, in Monterey Bay. Calif. Dep. Fish Game, Fish. Bull. 169:35–44.

White, W.
1983. A narrow boundary current along the eastern side of the Hawaiian Ridge; the north Hawaiian Ridge current. J. Phys. Oceanogr. 13:1726–1731.

Young, R. E., and J. Hirota.
1990. Description of *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) paralarvae with evidence for spawning in Hawaiian waters. Pac. Sci. 44(1):71–80.