

# Appendix B Potential Squid Pelagic Management Unit Species (PMUS)

## Neon Flying Squid (*Ommastrephes bartramii* Lesueur, 1821)

### General Description

*Ommastrephes bartramii*, commonly known as akaika, red squid, red ocean squid, red flying squid, flying squid, neon flying squid and Bartram's squid (among many other names), is the most broadly distributed species in the family Ommastrephidae with a circumglobal subtropical to temperate distribution (Murata 1990). The possibility of genetic interchange between disjunct populations in different hemispheres and oceans, apparently, has not been reported. Russian researchers (Dunning 1998), however, consider the North Pacific and North Atlantic populations to represent separate subspecies and the southern hemisphere populations to represent a third subspecies. The southern-hemisphere population, however, is discontinuous at the tip of South America and at the southeastern tip of Australia which suggests to Dunning (1998) that the South Pacific Ocean population is reproductively separate from the South Atlantic-Indian Ocean population. The northern limit of the population in the South Pacific is approximately 25°N latitude (Dunning 1998). This review is restricted to the North Pacific population where the species primarily occupies waters between 20° and 50°N latitude from near Japan to near the west coast of North America with highest population densities along the SAFZ from July-December (Murata 1990, Murata and Hayase 1993). In the North Pacific Ocean, *O. bartramii* is common as indicated by commercial catches that have reached over 300,000 mt/year. During summer and fall, *O. bartramii* is fished primarily between 36° and 46°N latitude and in winter most squid are thought to migrate south to the subtropics between about 25° and 35°N latitude where spawning occurs (Yatsu, et al. 1998, Ichii et al. in press). Within a few months of hatching the new generation, apparently, begins migrating northward (Seki 1993a).

Maximum size reported by Murata (1990) for North Pacific *O. bartramii* is 40.6 centimeter (cm) mantle length (ML) (1680 grams [g]) for males and 56.2 cm ML (5,790 g) for females. Although females grow to a much larger size than males, the length-weight relationships are indistinguishable and are given by the formula:  $W = (1.2799 \times 10^{-5})L^{3.1437}$  with L (length) in millimeters (mm) and W (weight) in g (Murata 1990). Mature males are found between 21-44 cm ML with most males larger than 30 cm ML mature and mature females between 37-57 cm ML with "a considerable number" mature between 40 and 50 cm ML and most mature larger than 50 cm ML (Yatsu et al. 1998). The life span of *O. bartramii* is estimated to be about one year.

### Eggs and Paralarvae

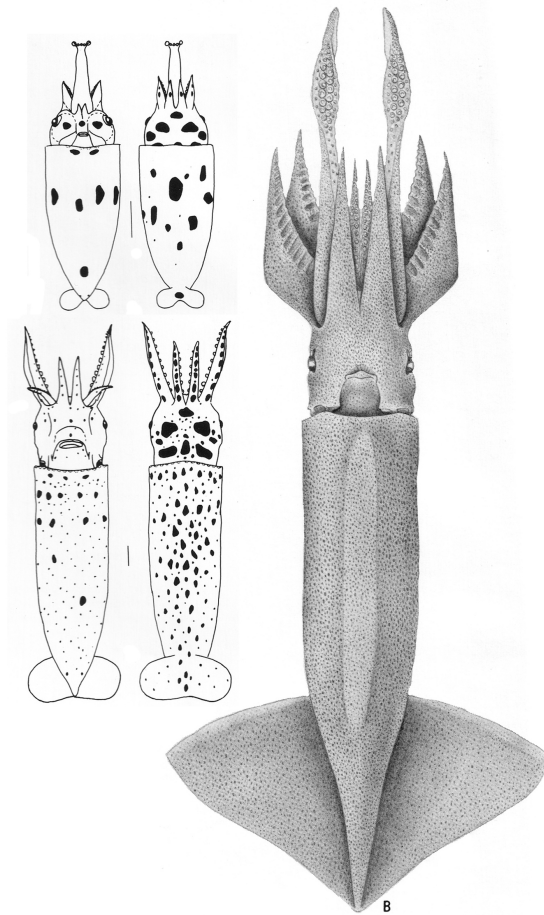
Most squids do not have a true larval stage but exhibit direct development and the term "paralarva" is used, therefore, to distinguish young in the near-surface plankton (Young and Harman 1988). The end of this stage is determined by both morphological and habitat changes.

Where known, nearly all squids spawn eggs in egg masses. Egg masses for *O. bartramii* have never been observed. In two other omastrephids (*Illex illecebrosus* and *Todarodes pacificus*) egg masses are gelatinous, nearly neutrally-buoyant spheres, about 50-80  $\mu$ m in diameter and contain up to  $20 \times 10^5$  eggs distributed throughout the egg mass (O'Dor and Balch 1985, Bower and Sakurai 1996). Presumably *O. bartramii* produces similar egg masses. Eggs of *O. bartramii* measure about 0.9 x 1.1 mm in size (Sakurai et al. 1995). The depths at which spawning occurs and the depths at which egg masses float and embryos develop are unknown for *O. bartramii*.

The distribution of paralarvae suggests that spawning does not occur in near-shore waters (Bower 1996, Yatsu et al. 1998, Bower et al. 1999). Spawning period, based on hatching dates determined by retrospective analysis of statoliths (calcareous structures in the balance organ, comparable to otoliths in fish) of subadult and adult squid, is from September to August (Yatsu et al. 1998). Spawning, therefore, occurs virtually all year long, but judging from the seasonal abundance of subadults (squid of commercial size are most abundant during June-September: Murata and Nakamura 1998), peaks in spawning exist. Hatchlings measure about 1.1 mm ML (Yatsu and Mori 2000).

Paralarvae appear to occur mostly in the upper 25 m during the day and night. Young and Hirota (1990) caught numerous *O. bartramii* paralarvae in surface plankton tows during the day and night. They also examined the vertical distribution of the paralarvae with a small opening-closing net. The latter series sampled the upper 200 m and caught 13 *O. bartramii* at 0-40 m during the day and 0-20 m at night. Saito and Kubodera (1993) caught small numbers of paralarvae in simultaneously towed vertical series of closing nets with the highest catch rates at 0-25 m but incidental catches at 50-75 m and 75-100 m.

Paralarvae have been captured over a broad stretch of the North Pacific Ocean from 140°E to 130°W between 25° and 35°N with a possible break in distribution at 170°E - 180° (Yatsu et al. 1998, Ichii et al. in press). In the region of the Hawaiian Archipelago, Bower (1994) caught paralarvae during February where SSTs (sea surface temperatures) were between 21°-24°C with peak abundance at 22.0°-22.5°C. All captures occurred south of the subtropical front at latitudes of about 21°-28°N. Young et al. (2000) confirmed the absence of paralarvae north of the subtropical front at latitudes in the Hawaiian region during February and the dominance of catches at SSTs around 22°C. In 2000 they found just hatched paralarvae as far south as 20°N off the windward side of the Island of Hawaii at SSTs of 23.4°-23.9°C. The following year *O. bartramii* paralarvae were virtually absent from these latter waters (personal observation, R. Young). The subtropical front meanders greatly during the winter and is ill-defined in the summer (Seki 2003). As a result, the possible relationship between the subtropical front and the spawning habitat is difficult to confirm and unknown for most regions and most seasons. The presence of paralarvae in Hawaiian waters or immediately northward is known for October-June (Young and Hirota 1990, Bower 1994, Yatsu et al. 1998, Ichii et al. in press). As the SSTs shift seasonally so does the spawning habitat as indicated by the distribution of paralarvae. Ichii et al. (in press) found paralarval distributions approximately confined to the 21°-26°C isotherms from October to May although the isotherms shifted latitudinally about 5° during this period. While the general geographic areas of the nursery grounds for paralarvae and SST-correlates are known for much of the year, the specific physical and biological conditions triggering spawning and favoring survival of paralarvae are unknown.



**Figure B.1 *O. bartramii* Paralarvae, Juveniles and Adults.**

In the case of one ommastrephid, *Illex illecebrosus*, however, O’Dor and Balch (1985) suggest physical parameters that might be necessary for spawning and embryonic development. They found that the egg mass was slightly negatively buoyant. An egg mass slowly sinking in the open ocean would encounter decreasing water temperatures (which increases water density) and would stop sinking when temperature equilibrium between the egg mass and the water is reached; but temperature equilibrium can occur quickly. Increasing water salinity (which would increase water density) encountered with depth also would stop sinking but it would take far longer (over two orders of magnitude longer) to reach equilibrium. A mid-depth salinity maximum could stop or slow the descent of an egg mass until hatching occurs. In Hawaiian waters a shallow salinity maximum, formed at the subtropical front, slowly submerges as it moves south (Roden 1991). This salinity maximum could retain an egg mass, spawned in lower salinity, near-surface water, within a relative warm-water environment (important for rapid egg development) that allows relatively easy access for hatchlings to surface waters. The shallow salinity maximum is present during the winter but is not apparent during summer.

Another physical factor that may be critical to paralarval growth and survival is temperature. Yatsu et al. (2000), noting that the El Niño years of 1993 and 1997 coincided with low stock

abundance, suggest that negative SST anomalies recorded during these years may have affected both the feeding and nursery grounds in their study area. Forsythe (1993) noted that cephalopods are poikilotherms with a Type 4 adaptation (i.e., metabolic rate varies with temperature with little or no compensation) and modeled the effect of temperature during the paralarval exponential growth phase on the loliginid squid, *Loligo forbesi*, and found that a 1°C increase in temperature during this critical period (90 days in this species) would result in a subadult twice as heavy and a 2°C change results in a 5 fold increase in subadult weight.

Ommastrephid squids have a peculiar paralarval stage in which the tentacles are fused together in an elongate "proboscis" that eventually splits apart to form normal tentacles. The presence of a proboscis suggests that these paralarvae have a unique, although unknown, method of feeding. Bigelow and Landgraf (1993) determined a growth curve for *O. bartramii* paralarvae, captured in February, based on statolith increment counts using both light and scanning electron microscopy (SEM). The curve they found was exponential and of the form  $ML = 0.331e^{0.103x}$  (ML in mm and x in days). They suggested that this growth curve applied to at least 12.1 mm ML at an age of 35 days. They found proboscis separation complete by 9.5-12.0 mm ML. They also estimated a size at hatching of 0.33 µm from the growth curve as they lacked paralarvae less than 18 days old. This hatching size subsequently proved (as the authors expected) to be much too small. A study by Bower (1996) using similar methods but without SEM found a growth curve of  $ML = 0.95e^{0.067x}$  for paralarvae captured in February. Yatsu and Mori (2000) re-examined paralarval growth rates using similar methods without SEM but for paralarvae captured in October and they were able to include hatchlings grown from artificial fertilization. The growth curve determined by Yatsu and Mori (2000) is  $ML = 1.139e^{0.063x}$ . They note proboscis separation was reported by Wormuth et al. (1992) to occur at 7 mm ML and that this size appears to coincide with a change from exponential to linear growth. They suggest that feeding habits must change at this point with the presence of functional tentacles. After separation, however, the tentacles are undeveloped and very small (L. Shea, personal communication with R. Young) indicating that considerable growth of the tentacles is necessary before they can participate in feeding. In addition, the more accurate measurements of Bigelow and Landgraf (1993) show tentacle separation occurred at a larger size. A change in feeding, if it does occur at 7 mm ML, may involve the replacement of the proboscis by the arms as the primary tool in food capture. The growth curve of all three studies gives a size of about 7 mm at 30 days of age in spite of the different capture seasons. In the absence of more complete data, the apparent change in growth rate at 7 mm ML can be considered the end of the paralarval stage.

### Juvenile

Juvenile squid are virtually absent from net, jigging or driftnet collections. Very little is known about the distribution of small squid between about 10 and 100 mm or virtually any other aspect of their ecology or biology. Yatsu and Mori (2000) reported the capture of 14 squid (52 - 164 mm ML) by dipnet at 28°-32°N. Harrison et al. (1983) commonly found unidentified ommastrephid squid, mostly smaller than 100 mm ML, in the diet of many seabirds in the Northwestern Hawaiian Islands (NWHI). Presumably many of these were *O. bartramii*. Seki and Harrison (1989) were able to identify *O. bartramii* as a minor component of the diet of the red-footed booby at French Frigate Shoals in the NWHI. Both studies suggest that juveniles occur in the region of the NWHI (ca. 23-28°N) in near-surface waters, presumably during the daytime. Judging from this limited data, the habitat of squid in this size range may not differ much, if any, from that of paralarvae.

Yatsu and Mori (1998) provide size at age data for squids about 30, 50 and 100 days old. A straight line drawn by eye through this data (i.e., their Fig. 4A) yields a growth rate of 1.8 mm/day. Using this growth rate, the growth rate jumps from 6.5% of the ML/day at 30 mm ML at the end of the exponential growth phase to 19.5%/day at 31 mm ML at the beginning of linear growth. Such a sudden jump is, of course, unrealistic. Nevertheless, as growth continues at 1.8 mm ML/day the daily rate of increase drops to about 8% within a week, and 5% in two weeks (45 days of age and about 33 mm ML) and 3% in four weeks (59 days of age and approaching 60 mm ML). This exercise suggests that during a 10 day period (corresponding roughly to juveniles of 7-25 mm ML) the relative linear growth rate of early juveniles exceeds the relative exponential growth rate of paralarvae. If true, then environmental conditions during this period may be especially important. Clearly more age data for juveniles is needed.

The size and age at the end of the juvenile period are unknown. Changes in the statolith occur at about the size and age that could mark this point in the life cycle. The width of statolith daily increments abruptly decreases from 5-7 $\mu$  at about increment 80-100 from the nucleus and is followed by a short zone (20-30 $\mu$ ) of indistinct increments then small increments, 1-2 $\mu$  to the edge of the statolith (Yatsu, et al. 1997). Yatsu et al. (1997) suggest that this transition probably corresponds to major changes in the ecology of the squid and Yatsu et al. (1999) suggest the juvenile period ends here. Yatsu et al. (1999) found that the end of the juvenile period for squid caught in 1995-1997 had mean ages from 87.4-92.9 days with a range of 70-113 days. Without considering a different growth rate for the paralarval stage, Yatsu et al. (1997) calculate that this short zone corresponds to mantle lengths of 96-220 mm by apparently using growth rates of 1.1 to 2.2 mm/day (see below). By including the paralarval period and using a single growth rate of 1.8 mm/day for post-paralarval growth and juvenile ages of 80-100 days, we calculate a range of 97 mm ML [(80 increments-days minus 30 paralarval days times 1.8 mm/day) plus 7 mm at end of paralarval growth] to 151 mm ML [(100 - 30 days + 10 days of transition) x 1.8] + 7] for size at the end of the juvenile stage. Therefore, a tentative working range for squid size corresponding to the short zone on the statocyst may be about 100-150 mm ML. Other than these possible statolith features, no morphological correlates are presently recognized that can mark the end of the juvenile stage.

### Subadult and Adult

The life history stages of squids include several terms not generally applied to other organisms. Because many squids are terminal spawners that spawn and die shortly after reaching maturity, the adult phase is often very short and most of the life span occurs in the normal juvenile stage. As a result the juvenile stage is generally divided into two steps, juvenile and subadult (Young and Harman 1988). The subadult stage extends from the end of the juvenile period (i.e., the size/age when most morphological characteristics of the species are attained) until maturity. Maturity is defined as the presence of eggs in the oviducts or spermatophores in Needham's sac.

### *Age and Growth*

Females attain larger sizes and grow faster than males (Yatsu 2000). Growth rates of squids are strongly affected by food availability and ambient temperature (Forsythe et al. 2001). Because of high growth plasticity, Yatsu (2000) recommends that data in age and growth studies not be fitted to *a priori* growth curves. Overall growth rates determined by dividing the squid length at capture

by the hatching date derived from statolith data indicate rates of 1.1 to 2.5 mm per day (Yatsu et al. 1997). This use of linear growth rates is not as risky as it might seem. Growth is exponential up to a size of around 7 mm ML, beyond that it appears to be linear (Yatsu and Mori 2000) at least until sexual maturity is reached. Tag and recapture rates for squid recaptured after 2 months or more give similar growth rates (1.85 - 2.44 mm/day; N=3) (Yatsu et al. 1997). Kasahara (1985) followed size modes of an apparently isolated population in the Sea of Japan and found essentially linear growth of about 1.9 mm/day from about 140 mm ML to about 420 mm ML (Murata 1990, Yatsu et al. 1997). While the variability in average growth rates found by Yatsu et al. (1997) is high, we must assume that the variability is even greater if one looks at daily or short-term growth rates rather than rates averaged over the life of the squid. For example, shorter average rates given by Araya (1983) for tag and release data show one squid recaptured five weeks after release appeared (size measurements were not exact) to exhibit no growth while a second released within two days of the first and recaptured after 11.6 weeks exhibited a growth rate of about 2.4 mm/day. Estimates of growth rates based on modal length data gave low rates of 1.1 mm per day and are considered less accurate due to complications in correctly tracking size modes in migrating squid (Yatsu, et al. 1997).

The fact that the linear growth data do not show evidence of slowing growth in mature *O. bartramii* may simply reflect an insufficient sample size of mature female squid. Obtaining adequate data will be especially difficult if the adult period is short. Linear growth means that relative growth slows as each growth increment, which is a constant, progressively becomes a smaller proportion of the increasing squid size. Therefore a mature *O. bartramii* could maintain linear growth while still providing energy for reproduction. Chen and Chiu (2003), however, based on back-calculated growth curves derived from statoliths, found that growth in a population of squid from the northeast Pacific Ocean that contained a few mature females did show a tapering of growth at larger sizes. They suggest that the slower growth could be due to reallocation of energy for maturation although they found a similar pattern in another population that lacked mature females.

Yatsu, et al. (1997) found that growth rates with hatch dates from January to August increased with the season although summer data were lacking for males. Murata (1990) summarizing results from modal length data, also concluded that growth was more rapid in summer-autumn than in winter-spring. Seasonal growth trends were most apparent in squid from 143°-146°E. Not surprisingly, growth rates of loliginid squid in culture have been shown to be strongly affected by temperature (Forsythe and Hanlon 1989).

The beginning of the adult stage for males, assuming the size at maturity for most males is 300 mm ML and the growth rate is 1.6 mm/day (midpoint between the range of male growth rates of 1.1 and 2.1 mm/day reported by Yatsu, et al. 1997), would be 188 days. The beginning of the adult stage for females, assuming the average size at maturity for females is 475 mm ML and the growth rate is 1.8 mm/day (midpoint between the range of female growth rates of 1.1 and 2.5 mm/day reported by Yatsu, et al. 1997), would be about 264 days. These data suggest that males mature at a younger age than females. Age determination from statoliths suggest a one-year life-span as mature males have been aged at 188-308 days (N=10) and mature females at 212-324 days (N=10) (Yatsu et al. 1998). If the maximum lifespan is 365 days for both sexes, then males would be in the adult phase of their life cycle for a much longer period than would females.

### *Population structure*

The population structure of *O. bartramii* has been extremely difficult to unravel because this squid is distributed over a large area, spawns virtually throughout the year and undergoes strong horizontal migration. Compounding this is a short one-year life-span and differential growth rates between males and females. Catches from driftnet fishers were usually processed on-board making biological data difficult to obtain (Murata et al. 1988). Catch data are also affected by weather, moonlight, and predators, and size data can often be biased by the type and size of fishing gear.

At any locality north of the subtropical region where the squid are common, often more than one size mode is present. Murata (1990) attempted to quantify four possible groups of females and three of males that had long been recognized (at least from the work of Murakami et al. 1981). The groups are known as SS (extra-small), S (small) and L (large) for males and females and LL (extra large) for large females which attain a much larger size than the largest males (a counterpart for the LL group in males cannot be recognized: Murata 1990). Murata identified each group by size and month which enabled following monthly progressions of size modes, although his classification was incomplete for some months and some sizes. Murata (1990) and Murata and Hayase (1993) noted that the SS, S and L groups might represent a common cohort with different peaks of hatching during winter and spring. A division of the population into subpopulations at approximately 160-170°E had been generally recognized since the work of Murakami et al. (1981) mostly due to low catches in this region and differences between the size composition of the catch to the east and west (Murata 1990). The subpopulation on the eastern side was thought to develop in the autumn and that of the western side in the spring (Murata 1990; Fig. 1 in Murata and Nakamura 1998).

Yatsu et al. (1997), using statolith data to determine hatching dates of adult and subadult squid, cast doubt on the validity of the alphabetical classes by noting that spawning occurred virtually throughout the year and growth rates were faster than those determined from the alphabetical size modes. Yatsu et al. (1998) revised the view of the population structure mostly on the basis of data from research cruises and with statolith-determined squid ages. They recognized two seasonal cohorts: one an autumn cohort (comprising the LL group) with a hatching period from September to February and a winter-spring cohort with a hatching period primarily from January to May but extending to August. That a male counterpart to the autumn cohort has not yet been recognized from statolith data (Yatsu et al. 1998) is unfortunate but not surprising; LL males and females probably do not occupy the same waters much of the time, so absence of LL males in the statolith data could be due to chance. Chen and Chiu (2003), however, also failed to distinguish LL males although males sampled hatched between September and March.

The division by Yatsu et al. into two seasonal cohorts appears to be supported by their finding of two modes in the size of mature squids: mature females collected during the autumn-winter period (between September and February) were larger (mode ca. 53 mm ML) than those collected in the spring-summer period (between March and August)(mode ca. 43 mm ML). Also, they were able to recognize the autumn cohort by the monthly progression of its mantle-length modes. Yatsu et al. (1998) found the autumn cohort to be more abundant in the central and eastern Pacific Ocean east of 170°E (170°E approximately marks the position of the Emperor Seamounts) but they apparently coexist throughout the North Pacific Ocean. Squid of the autumn cohort taken from the

same waters as the squid of the winter-spring cohort have different abundances of various nematode and cestode parasites, a finding which supports the presence of different cohorts (Yatsu et al. 1998).

Indeed, Nagasawa et al. (1998) and Yatsu et al. (1998) divide the North Pacific Ocean into three zones based partly on the occurrence of these parasites in *O. bartramii*: a western region bounded by the 170°E longitude, a central region between the 170°E and 160°W longitudes and an eastern region east of 160°W. The winter-spring cohort has one stock in the western region and one in the combined central-eastern region. The autumn cohort has one stock in the eastern region and one in the central region; this cohort is rare in the western region and has an uncertain relationship to the central stock. Yatsu et al. (1998) suggest that the stocks are not genetically separated due to the overlapping hatching dates. In addition, they suggest that male-female size differences, which could affect mating, are mitigated by the large variability in growth rates. Chen and Chiu (2003), however, based on back-calculated growth-curves derived from statoliths and statolith radius to mantle length relationships, recognized the two seasonal cohorts, and also suggest that females (as well as males) of the winter-spring cohort represent separate populations in the central-eastern and western regions. In addition, they examined large females (autumn cohort) from the western region but found no differences between these and their counterparts in the central-eastern region. They suggest that large females of the western region are spawned in the central-eastern region. Katugin (2002) also suggests genetic differences using protein electrophoresis. Subsequent studies by Katugin and a co-worker (per. comm. from J. Bower to R. Young) based on alloenzyme differentiation found no significant differences between eastern and western regions and no differences between size groups in the Northwest Pacific Ocean. Japanese scientists at the National Research Institute of Fisheries Science are presently using mtDNA sequencing to separate Pacific and Atlantic populations and hope eventually to identify local stocks with this technique (Bower 2004).

The mechanism responsible for the larger size of the autumn cohort (i.e., maximum > 55 mm ML vs 46 mm ML (Bower 2004)) is unknown (Yatsu et al. 1998). Ichii et al. (in press) suggest that paralarvae of both seasonal cohorts exhibit similar conditions of low environmental productivity. However, by the time the squid of the Autumn cohort are juveniles, a Transition Zone Chlorophyll Front has moved south through their habitat bringing higher food availability and allowing higher growth rates than in the case of juveniles of the Winter-Spring cohort which remain in low-productivity waters. The advantage of higher productivity waters for the Autumn cohort remains throughout much of the subadult stage as well. The result is the distinct size separation between the cohorts. Chen and Chiu (2003), however, found that the two size cohorts (LL and S) in their study in the eastern region had peak hatching periods separated by only two months (October and December) and with broad overlap in time of hatching of all squid examined. The latter study suggests that if the productivity hypothesis of Ichii et al. is correct, the spatial and temporal differences that lead to a size advantage may occur on rather small scales. The size modes within the winter-spring cohort, as indicated by Murata (1990), may relate to variation in success of young during different (and presumably variable) periods of the spawning season and/or to subsequent differences in growth rate.



## Horizontal Migration

There are two aspects to the north-south migrations of *O. bartramii*. First is a seasonal geographic shift of the major squid concentrations at their northern-most locations which are assumed to be major feeding grounds. In June the major concentrations (as determined by commercial fishing) are at 35°-40°N; during August-October they shift northward to 40°-45°N (i.e., about 2° latitude/month), then during November-December they shift gradually southward (Murata and Nakamura 1998). An example of a latitudinal peak in squid concentrations is seen in the following example. Chen and Chiu (1999) using data from an experimental fishing cruise that ran latitudinal and longitudinal transects from about 38°N to 44°N and 150°-170°W during July and August of 1997, found the catch-per-unit-effort (CPUE) averaged about 5-8 kilograms per hour (kg/hr) between 38° and 42°N. The CPUE began increasing at 43°N and peaked at 100 kg/hr at 44°N which lay in the northern part of the SAFZ.

Second, and superimposed on the first movement, is an ontogenetic migration. *O. bartramii* migrates northward, as it grows, from a subtropical hatching site to the feeding grounds of the subadults near or within the SAFZ and then returns to subtropical waters for mating and spawning (Seki 1993b). The two population movements are not the same as spawning occurs virtually throughout the year. Even during the major spawning season evidence of the two migrations can be detected. If one calculates the growth rate of *O. bartramii* from the seasonal and northward progression of its different size modes, an erroneously slow growth rate is obtained (Yatsu et al. 1998); therefore the northward movement of individuals is somewhat different than the northward movement of modes. Presumably squid migrate north toward the feeding grounds as they grow but the location of the feeding grounds shifts with the changing season and squid adjust accordingly. The distribution patterns are further complicated by some size and sex segregation.

Because the ontogenetic migration occurs during a one year life-span, a gradation of increasing squid size should be encountered with increasing latitude as the ontogenetic migration progresses northward. Superimposed on this gradient are the southward migration of large squid to the spawning grounds and the shifting location of the subadult feeding grounds. Because the northward migration should generally take longer due to the small size of the squid and the population should be more numerous at these sizes, the north-moving squid should generally (all else being equal) dominate the catches. This simple model is complicated by, among other effects, seasonal and local cohorts of differing abundance and areal effects of size segregation. Nevertheless, increases in squid size with increasing latitude are usually found (Araya 1983). To site one example, Murata et al. (1988) reported catches in July from research driftnets, with a range of mesh sizes, and jigging between 160°E and 172°W and 37° - 41.5°N. This latitudinal range included the TZ, the Subarctic Boundary and the SAFZ with surface temperatures ranging from 24° to 12°C. At 37°N squid ranged from 14-19 cm ML (modes at 14, 17 and 18 cm). At 38°30'N the range was 17-27 cm ML (modes at 18 and 21 cm); at 40°N the range was 20 - 25 cm (modes at 20 and 24 cm); at 41°30'N the range was 27-42 (modes at 27, 38 and 41 cm).

In general, according to Murata and Nakamura (1998), the winter-spring cohort is distributed mainly within the Subarctic Boundary and SAFZ during summer and fall. Females tend to move into this region before males and southward migration is thought to occur mostly in October to November for males and November to December for females. The females of the autumn cohort are found largely in the SAFZ in the spring to summer and males are found further south. Males

apparently start migrating south in July and females in September. Males never seem to occur in the high abundance of females in the northern-most areas (e.g., Figs. of Yatsu et al. 1998). Therefore, the northern, seasonally shifting population abundance peak appears to be composed mostly of females. Murata et al. (1988) obtained samples from the driftnet fishery taken mostly from 39°-46°N, 170°E-145°W, which presumably follows the abundance peak, from June-December during 1983-85. The catch was mostly females with a 3-year average of 2.4% males. Males and females clearly show some different spatiotemporal distribution patterns. As another example, a research cruise in 1988 (170°E - 180°), found females dominating the catch in the northern area of the SAFZ (ca. 41-43°N), males dominating in the southern area of this zone (ca. 40°N) and males only in catches at 35°N (Murata and Nakamura 1998). More information is needed on the relative distribution of the sexes and on causes of size and sex segregation. Do large squids just migrate further or do they exclude smaller squids from the same region? Do the squid school by size and sex? These and other problems (e.g., fishing-gear selection) of real or apparent sex segregation make determining sex ratios difficult.

Yatsu et al. (1998) found mature females as far as 42°N and mature males as far as 45°N. Mature females were commonly present at stations south of 35°N and males were commonly present at stations south of 43°N. While the occurrence of mature squid is broad, their relative abundance peaks south of 35°N (Murakami et al. 1981).

### *Swimming Speed*

Average swimming speeds were measured using ultrasonic transmitters attached to free-swimming squid by Nakamura (1993) for squids apparently on the spawning grounds (26°-28°N). Swimming speeds ranged between 19 and 25 cm/s over the entire tracking period (three squid, 9, 23 and 36 hrs.) for squids of 44-46 cm ML but swimming was not always in one direction. Yoshida et al. (1990) tracked three females that swam consistently in a southeasterly direction from about 35°N and were apparently migrating. Their average speeds varied from 25-30 cm/sec or 54-74% of their ML (squids were females of 38-42 cm ML). At 30 cm/sec a squid would require about two months to travel directly south from the feeding grounds (ca. 45°N) to the spawning grounds (ca. 30°N) disregarding possible effects of currents. The paper by Murata and Nakamura (1998) on ultrasonic tracking did not provide data on swimming speed.

The tag and release study of Murata and Hayase (1993) reported 11 migrating squids that had been released in May-June and recaptured mostly between one and three months after release. These squid traveled in various directions between NNW and ENE at a combined average speed of 11.8 km/day (14 cm/sec). Two of these squid traveled (one ENE and the other NE) for an average distance of 594 miles at an average speed of 23.1 km/day (27 cm/sec). The sizes of these squid at release are not known but, based on the time of release and direction of movement, presumably the squid were considerably smaller than those tracked by ultrasonic transmitters.

### *Spawning*

Many details of spawning that are critical to understanding the population dynamics of *O. bartramii* are unknown. Cephalopods exhibit five spawning patterns (Rocha et al. 2001). Among ommastrephid squids the best understood strategy is that of *Todarodes pacificus* which have a "spawning once" strategy (terminal spawning) (Ikeda et al. 1993). Squid with this strategy have:

synchronous ovulation, no ovulation during the spawning period, monocyclic maturation of oocytes (i.e., a single cycle of ovarian development) and spawning during a short period near the end of life (i.e., no growth occurs) (Rocha et al. 2001). A closer relative of *O. bartramii*, *Sthenoteuthis oualaniensis*, appears to be a "continuous spawner" (Rocha et al. 2001) with the following characteristics: continuous asynchronous ovulation, ovulation during the spawning period, monocyclic maturation of oocytes, spawning over an extended period with intermittent spawning events (i.e., as the oviducts fill, they are emptied) and somatic growth during the period of spawning. *O. bartramii* probably utilizes this latter strategy. However, the evidence is not conclusive and is reviewed here. The size-frequency of oocytes in the ovary of mature *O. bartramii* shows an exponential decrease in numbers from small to large oocytes (Young et al. 1997). This indicates continuous asynchronous ovulation. Mature female *O. bartramii* exhibit great variation in the state of fullness of the oviducts and this shows no relationship to mantle length (Young et al. 1997, Yatsu et al. 1998). In addition, the weight of the nidamental glands of mature females varies with the weight of the oviduct rather than the mantle length, suggesting that the nidamental glands which form much of the jelly for the egg mass, fluctuate in size as the oviducts are filled and emptied (Young et al. 1997). These two latter features both suggest monocyclic maturation of oocytes and continuous spawning. Finally, great variation exists in the size of mature females suggesting that growth occurs during the period of spawning. These data are not conclusive due to ambiguities created by variation in the size of females reaching maturity and possible unknown variation in the rates of ova production (Young et al. 1997).

Assuming that *O. bartramii* is a continuous spawner, the length of the spawning period and the number of spawning episodes must be known in order to determine total fecundity. Neither of these are known. The batch fecundity (number of ova in both oviducts) is known to reach at least  $1.4 \times 10^6$  eggs in a female of 590 mm ML and  $1.3 \times 10^6$  in a 545 mm ML female (Young et al. 1997).

#### *Vertical distribution*

Judging from the methods used in commercial fisheries (jigging-usually upper 50 m, driftnets-upper 10 m) *O. bartramii* commonly occupies depths of 0 to 50 m at night at the Subarctic Boundary (Murata 1990). At 37°N latitude from 160°E to 172°W small *O. bartramii*, estimated at 140-180 mm ML in numbers up to several hundred at a time, have been observed gliding above the surface of the water during nighttime and daytime suggesting the habitat for squid in this size range is in near-surface waters during the day and night (Murata 1988). The "flying" portion of the name "neon flying squid" came from previous observations of this sort (see Clarke 1966).

A few squid have been tracked by ultrasonic telemetry. Murata and Nakamura (1998) acoustically tracked 10 apparently female squid in the region of the SAFZ (ca. 42°-45°N). At night the squid swam at depths of 0- 40 m within the mixed layer. During the day the two longest records appear the most reliable: the first squid (48 hrs) swam at depths of 150-200 m during the daytime (10°-6°C) and the second squid (22 hrs) swam at depths of 160-300 m during the daytime (7°-4°C). A few squid stayed near the surface during the daytime.

Nakamura (1993) acoustically followed three mature females in subtropical waters (ca. 26°-28°N). One stayed at depths between 400 and 700 m in the day and mostly at 40-70 m at night with occasional excursions to the surface. The temperature at 600 m was 9°C. The second squid didn't

provide much useful information and was lost after about 8 hrs. The third squid spent the day at depths greater than 680m (limit of the working range of the transmitter). The actual records show the squid between about 700 and 900 m but are unreliable. The squid migrated up to depths mostly between 50 and 70 m at night then in the late night and early morning the behavior became erratic and the squid was lost. The greater daytime swimming depths of squid in subtropical waters presumably is related to the greater clarity of these waters, which requires that the squid swim much deeper to reach the same light levels (Murata and Nakamura 1998).

Young et al. (1997) found a predominance of mature males over mature females in Hawaiian waters during February and suggested that this may be due to greater swimming depths of females making them less susceptible to jig fishing. This suggestion is supported by the tracking data of Murata and Nakamura (1998) and submersible observations on a related squid, *Sthenoteuthis oualaniensis*, in the Arabian Sea. In the latter case medium-sized females were found in the 0-100 m depth range at night while large females (in the size range of mature *O. bartramii* females) were seen at depths of 50-500m (Bizikov 1995).

Presumably *O. bartramii* can on occasion descend to much greater depths than recorded above. Clarke (1966) reported that *O. bartramii* in the North Atlantic had tentacles caught in reversing thermometers as deep as 1490 m. Submersible observations in the North Atlantic found *O. bartramii* at 540-1,050 m by day and mostly in surface waters at night with a few individuals to 300 m depth; in the South Atlantic *O. bartramii* was found at 530-950 m, but mostly at 750-850 m by day and near the surface at night (squid ranged from 15-45 cm ML)(Moiseev 1991).

### Prey and Predators

#### *Prey*

Seki (1993b) examined stomach contents of *O. bartramii* (N= 174, mean length 322 mm ML, SD = 98.1, all immature, about 70% female) caught by gillnet within the SAFZ during the summer. He found many squid with empty stomachs (nearly 80%) and a high incidence of apparent cannibalism. The prey consisted about equally of cephalopods and fish whether considering weight or frequency of occurrence. Most fishes were not identifiable but those that were consisted largely of mesopelagic myctophids and stomiiforms and the epipelagic saury, *Cololabis saira*. About a third of the cephalopod prey were unidentifiable but nearly 60% of the identifiable squid consisted of *O. bartramii*; but Seki suggested that the cannibalism could be an artifact of the sampling technique. Seki (1993b) found remains of partially cannibalized *O. bartramii* entangled in driftnets and suggested that free-swimming squids were attacking those caught in nets. If the *O. bartramii* are eliminated from the samples, squid then would comprise 32% of the diet by weight.

Seki (1993b) also examined 42 mature females captured in February by driftnets in the general vicinity of 30°N latitude (ca. 25°-34°N), in the general region of the subtropical front. About 30% had empty stomachs. The diet consisted of predominately fish and squid. If *O. bartramii* and unidentified ommastrephids are eliminated from the data, squids comprise 44% of the diet. These two studies found no significant regional differences in the diets of the squid when using the categories fishes, squid, and cannibalized *O. bartramii* (Seki, 1993a).

The most detailed study of feeding in the TZ and the SAFZ was by Watanabe et al. (2004). They examined both the Autumn and Winter-Spring cohorts in May and July. In May the Winter-Spring cohort was in the TZ, mostly between 15-19 cm ML, and fed mostly on planktonic crustaceans (euphausiids and amphipods) but in July this cohort was still in the TZ and fed mostly on fishes (especially *Maurolicus imperatorius* a mesopelagic boundary species that is especially abundant in the region around the Emperor seamounts and the Shatsky Rise area which were near the study area). The changeover from crustaceans to fish occurred around a size of 20 mm ML. The Autumn cohort in May in the TZ fed mostly on fishes and cephalopods with fishes more common in the diet but with the two groups about equal in weight contribution to the diet. The fishes were mainly myctophids, especially *Symbolophorus californiensis*, and the squids were mainly gonatids and the onychoteuthid, *Onychoteuthis borealijaponicus*. In July most members of the Autumn cohort had left the TZ and those that remained fed on fish, mostly *M. imperatorius*, as the other fish and squid prey had moved northward to the Subarctic Transition Zone (SATZ) or beyond. The major portion of the Autumn cohort in July was found in the SATZ where they again fed on fishes and squids with fishes more common in the diet but squids comprising more of the biomass. The dominant fish were *S. californiensis* and the Subarctic bathylagid, *Bathylagus ochotensis*. The dominant squid was *O. borealijaponicus* and species of *Abraliopsis*. Two of the fishes, *B. ochotensis* and *Protomyctophum thompsoni*, found in diet during this study are non-migrators that remain in deep water (300-600m and 200-400 m respectively) day and night. *O. bartramii*, therefore, feeds at depth (presumably during the day) as well as near the surface at night. Based on estimates of the daily ration needed for *O. bartramii* (6% body wt/day), the biomass of this squid in the SAFZ (240-610 mg wet weight/m<sup>2</sup>) and the biomass of vertically migrating myctophids (5.2 g wet weight/m<sup>2</sup>), the authors conclude that *O. bartramii* consumes 4.9-12.4% of the total estimated biomass of vertically migrating myctophids during the summer.

Murata (1990) also found that small, immature squid prey more heavily on crustaceans. In squid 150-190 mm ML stomachs contain 44% crustaceans, in squid 200-240 mm ML stomachs contain 21% crustaceans and in squid larger than 240 mm ML stomachs contain 4-7% crustaceans.

Off Japan Araya (1983) found mostly fishes in *O. bartramii* stomachs with myctophids dominant and followed by sardines, mackerel larvae and sauries. Squids were 18-30% but this included a high proportion of cannibalized *O. bartramii*. Crustaceans fluctuated widely between 2-18% with the higher percentages in young squid. Naito et al. (1977) had found very similar results off Japan but noted nearly 40% empty stomachs.

Pearcy (1991) in a general study of the biology of the transitional region, noted that *O. bartramii* fed almost exclusively on the gonatid squid, *Berryteuthis anonychus*, at 44°N during a gill net survey along 155°W. At more southernly stations the diet consisted variously of fishes, squids, pteropods, heteropods and crustaceans.

Parry (2003) in a detailed study of feeding of mostly adult *O. bartramii* captured within or south of the subtropical front near Hawaii during winter (February) found the diet consisted almost exclusively of fishes and squids with fishes being much more abundant. Myctophids were the most common fishes in the diet and, among squids, onychoteuthids were the most common but *O. bartramii* took a wide variety of mesopelagic fishes and squids with no one species of fish accounting for more than 10% of all fishes eaten. To determine the trophic level of *O. bartramii*, Parry examined the  $\delta^{15}\text{N}$  content of the mantle muscle. Paralarvae had an average of 6.4‰, squids

of 75-100 mm ML had an average of 6.9‰, those of 200-300 mm ML had 11.1‰ and those of 300-570 mm ML had about 12.0‰. This odd logistic shape of the data was supported by retrospective analyses of  $\delta^{15}\text{N}$  content of eye-lens tissue from single squids. His baseline data from filtered seawater was 2.8‰ and assuming a 3.4‰ increase per trophic level he placed large females at about trophic level 4. He acknowledged that many variables can affect the  $\delta^{15}\text{N}$  values and that the 3.4‰ change per trophic level was inconsistent in his data. Nevertheless, the data provide a working model of the trophic position of this squid. Different trophic levels were determined for *O. bartramii* by Aydin et al. (2003) from their trophic model of the Subarctic ecosystem (the SAFZ included) based on stomach contents. They place *O. bartamii* at a trophic level of 5.3 in the eastern Subarctic region and 5.1 in the western region.

### *Predators*

Many marine mammals prey on squid. There are 47 species of marine mammals in the North Pacific Ocean north of 30°N, and over 10 million individuals that consume over 13 million metric tons of prey during the summer (Hunt et al. 2000). *O. bartramii* is certainly an important prey for many of these species but information is limited. The percent of the diet consisting of *O. bartramii* for the following marine mammals was used for the trophic model of the Subarctic ecosystem by Aydin et al. (2003) for the eastern Subarctic area: sperm whale (34%), toothed whales (4.6%), fin whales (2.3%), sei whales (2.3%), northern fur seals (13.7%), elephant seals (18.3%), Dalls porpoise (20.6%), white sided dolphin (11.4%), right whale dolphin (22.9%). Values were considerably lower in the western Subarctic area. Mori et al. (2001) found *O. bartramii* to be an important prey of the northern fur seal in the Central North Pacific Ocean.

In the North Pacific Ocean north of 30°N there are 135 species of seabirds and over 200,000,000 individuals (Hunt et al. 2000). Many feed on squid. In the PICES (North Pacific Marine Science Organization) tropical zone (30°N to about 45°N) some albatrosses and shearwaters are estimated to consume over 350,000 metric tons (mt) of squid during the summer, with *O. bartramii* the dominant prey (Hunt et al. 2000).

Swordfish are known to feed heavily on squid, often predominately ommastrephid squids (Toll and Hess 1981, Stillwell and Kohler 1985). Ommastrephid squids, especially *O. bartramii*, appear to be important in the diet of swordfish captured near 30°N latitude in February where swordfish may be feeding on concentrations of spawning squid (Seki 1993a).

Seki (1993a) found that the diet of blue sharks caught within the SAFZ by surface longlines during the summer in the size range of 66-155 cm precaudal length, consisted of 55% *O. bartramii* by weight.

In general, most large fishes and toothed marine mammals in the subtropical to Subarctic regions of the North Pacific Ocean are known to feed on squids but the species of squids usually have not been identified (Seki 1993a).

### Habitat

The general habitat of *O. bartramii* in the North Pacific Ocean appears to be approximately 20-50°N in oceanic waters from Japan to North America with the highest densities of commercial-

size squid found along the SAFZ (Murata and Hayase 1993). *O. bartramii* rarely occurs off east China or in the Japan, Okhotsk and Bering Seas (Araya 1983). More precise boundaries are difficult to define. Based on Japanese fishery records, the population has a more northerly distribution east of 170°W and major concentrations occur westward during October-December (Murata and Nakamura 1998). That is, in December catches east of 160°W decline greatly and are absent west of 180° (Murata and Nakamura 1998). Kubodera et al. (1983) suggest that the species does not enter the Subarctic Domain north of the SAFZ. Murakami et al. (1981), however, show good catches as far as 49°N, 139°W, well into the Subarctic Domain in 1978-9. In the Western Pacific Ocean Murakami shows catches as far as 46°N at 162°E and just over 44°N off the Kuril Islands at about 149°E.

In the central Pacific Ocean the most southerly record we are aware of is a mature female taken just south of the Hawaiian Archipelago at 17°S and about 160°W (Young et al. 1997). In the eastern North Pacific Ocean Wormuth (1976) reported a female (122 mm ML) at 27°N, 120°W. Murakami et al. (1981) report mature females from about 25°N at 142°E and about 24°N at 170°E.

The northern end of *O. bartramii*'s distribution generally does not extend beyond 11°C SST although it is known from SSTs as low as 9°C (Yatsu 1992, Yatsu and Watanabe 1996) and good catches have been made at 10°C in November (Yatsu 1992). For example, fishing effort during 1987 occurred with SSTs ranging from 10°-27°C with 97% of the effort at 11°-17°C and 0.1% at 8°-9°C (Murata and Hayase 1993). Low SSTs probably do not directly limit the distribution of the squid as they can enter temperatures of at least 4°C and probably less at depth during the day (Murata and Nakamura 1998). *O. bartramii* is mostly fished where SSTs lie between 13°-18°C (Yatsu et al. 1993). Temperatures at the southern end of the distribution are less well known. Bower (1994) reported paralarvae at SSTs up to 24.9°C in Hawaiian waters. Hayase (1995) reported paralarvae from about 26°N at 158°E at a SST of 26.6°C. Presumably the habit of *O. bartramii* of descending into deep waters during the day prevents their occurrence in neritic waters.

### Status of the Stock

The combined annual catch by the Japanese, Taiwanese and Korean fisheries for 1985-1990 ranged from 248,000-378,000 mt (328,000 mt ave.)(Murata and Nakamura 1998). *O. bartramii* has been fished commercially in the North Pacific Ocean since 1974 (Yatsu et al. 2000). An intense fishery for *O. bartramii* began in 1978 with the introduction of driftnet fishing, and driftnet fishing dominated the fishery until the end of 1992 when a moratorium on large-scale driftnet-fishing was instigated (Yatsu et al. 2000). Catch rates from driftnet fishing greatly exceeded those of jigging when fishing in the same area (1.5 - 3.8 times greater) (Murata 1990) and driftnet catches represented about 87% of the Japanese total catch between 1985-1990 (Murata and Nakamura 1998). Prior to the moratorium data were insufficient to assess the population size, but there was some indication from declines in the stock size index and the size of individual squid that the population in the eastern region might be declining (Murata 1990). The CPUE for the Japanese driftnet fishery, however, showed a peak in 1990 and good values in 1991 and 1992 (Yatsu and Watanabe 1996). The major fishery, before the moratorium, operated primarily from June through December with most fishing occurring in the SAFZ (Araya 1983, Murata 1990, Murata and Hayase 1993). The current jigging fishing grounds lie at about 40-42°N and 150°-170°E (Yatsu et al. 1997). Research catches using jigging and small-size driftnets

starting in 1980 show high catches beginning in 1994 indicating that the population recovered rapidly after the termination of commercial driftnet fishing (Yatsu et al. 2000). In the western region total catches in the jigging fishery ranged from 50 kilotons (Kt) to 80 Kt during 1994-1998 and fell to 30 Kt in 1999 and 2000 (Yatsu 2003 cited in Bower 2004). In the central region, beginning in 1996 the Japanese *O. bartramii* jigging fishery showed increasing catches to 1998 then declining catches (1997 - 12 Kt, 1998 - 21 Kt, 1999 - 12 Kt, 2000 - 5 Kt. Numerous Chinese jigging vessels, estimated to be about 400-600 in number with a catch equal to or greater than the Japanese catch), along with Korean and Taiwanese vessels operating in the general area of the Japanese fishing grounds may contribute to the declining catches (Ichii 2003 and Yatsu 2003, both cited in Bower 2004).

The total biomass for *O. bartramii* in the North Pacific Ocean is uncertain. Aydin, et al., (1993), however, used estimates of 1,678 Kt for the population size of *O. bartramii* for their Subarctic gyre models. Ichii (2003 cited in Bower 2004) estimated, with uncertain reliability the Maximum Sustainable Yield (MSY) (his "resource") of the autumn cohort for the year 2000 to be 370 Kt and he roughly estimated its biomass on the driftnet fishing grounds during the driftnet period at 240-610 Kt. Ichii (2003 cited in Bower 2004) also noted that the catch of the winter-spring cohort in the central and east region during the drift net period was 10,000 to 60,000 tons, but that the current MSY is not known. Osako and Murata (1983) estimated the sustainable catch for *O. bartramii* west of 170°E (i.e., for the west stock of the winter-spring cohort) at 80-100 Kt. The reliability of this estimate for the present resource (i.e., over 20 years later) is uncertain (Bower 2004). Considering the uncertainty of the MSY estimates and the uncertainty of the present fishery yield, the position of the population on the yield curve cannot be determined.

The CPUE has fluctuated greatly since 1995 and this may be due to changing environmental conditions in the North Pacific Ocean (Ichii 2003 cited in Bower 2004).

## **Diamondback Squid (*Thysanoteuthis rhombus*)**

### General Description

*Thysanoteuthis rhombus*, commonly called the diamondback squid, diamond-squid, sode-ika, taru-ika, chipirone, and chipilona among others, is the sole member of the family Thysanoteuthidae. *T. rhombus* has a distinctive morphology and its phylogenetic relationships with other squids are unknown. It is found in tropical and warm-temperate waters throughout the world's oceans, but is rarely abundant (Nigmatullin and Arkhipkin 1998); although it supports small fisheries in the Sea of Japan and in waters around Okinawa. *T. rhombus* is of interest to pelagic fisheries in Hawaii because of its large size and desirable eating qualities which make the capture of low numbers valuable. The usual maximum size is about 850 mm ML for females and 800 mm ML for males with body weight up to 20-24 kg (Nigmatullin and Arkhipkin 1998). These authors suggest that individuals can reach 1000 mm ML. Kawasaki and Kakuma (1998) report a maximum size of 900 mm ML off Okinawa. Miyahara and Gorie, in press (mentioned in Bower 2004) report a length to weight formula, based on 10, 432 squid of 194-745 mm ML from the Sea of Japan, with mantle length (L) in mm and total weight (W) in grams (g) of  $W=(4.008 \times 10^{-5})L^{2.982}$ . Nigmatullin and Arkhipkin (1998) present a similar curve based on squid from the Atlantic and Eastern Pacific ( $W=0.056L^{2.89}$  with L in cm). Sexual differences in this length/weight relationship



were not apparent. Males mature by 450 mm ML and females by 650 mm ML (Nigmatullin and Arkhipkin 1998).

*T. rhombus* probably has the thickest mantle of any muscular cephalopod. Mantle thickness reaches 40-50 mm in individuals of 700-800 mm ML and the mantle weight reaches 60-85% of the total weight (Nigmatullin and Arkhipkin 1998). Another unusual feature is the presence of very large fins that extend the full length of the mantle.

Very little is known about the population structure of *T. rhombus*.

### Eggs and Paralarvae

Egg masses of *T. rhombus* have been reported floating at the surface of the tropical Atlantic and Pacific Oceans on many occasions (e.g., Suzuki et al. 1979, Young and Vecchione 1996, Nigmatullin and Arkhipkin 1998, Billings et al. 2000, Guerra et al. 2002, Bower 2004). A submersible observation in calm water showed one egg mass floating about 10 cm below the ocean surface (pers. obs., R. Young). The egg mass has a sausage-shape with a length of 600-1800 mm and a diameter of 110-300 mm (Nigmatullin et al. 1995). Compared to ommastrephid egg masses, the egg mass of *T. rhombus* is tough and resilient. Near the surface of the mass, the eggs are arranged in two adjacent rows that spiral around the entire cylindrical egg mass like a coiled spring. The number of eggs varies from 32,000 to 76,000 (Nigmatullin et al. 1995), 24,000 to 44,000 (Guerra et al. 2002) or 180,000 (Billings et al. 2000). Batch fecundity is estimated to be up to 140,000 eggs (Nigmatullin et al. 1995). Eggs are 1.6-1.8 mm in diameter (Nigmatullin and Arkhipkin 1998). Sabirov et al. (1987) state that shortly before hatching occurs the egg mass loses its buoyancy and sinks. Confirmation of sinking is needed by other studies.

Paralarvae have a distinctive appearance and are easily recognized. Nevertheless, little is known about their precise vertical distribution. They presumably leave the egg mass in near-surface waters. Paralarvae of various sizes are captured in the upper 100 m (Bower et al. 1999). Around the Hawaiian Archipelago, Bower et al. (1999) found the paralarvae were part of an “oceanic” assemblage of paralarvae rather than an “island-associated” assemblage. They ranked 23rd in abundance of the 57 species of paralarvae captured.

The size of paralarvae at hatching was estimated from Clarke (1966) at 1.6 mm ML. Nigmatullin and Arkhipkin (1998) give a hatchling ML of 1.0-1.3 mm. Watanabe et al. (1998) measured hatchlings at 1.4-1.6 mm ML. Growth rates of paralarvae have not been studied. Nigmatullin and Arkhipkin (1998) suggest the end of the paralarval phase occurs at 16-18 mm ML when arms II and III reach 80-115% of the ML and the fins reach 80-85% of the ML. Wakabayashi et al. (2003) suggest that the end of the paralarval stage may occur at 6-8 mm ML when development of the beak rostrum, disappearance of cilia on the lips and development of suckers on the distal third of the arms may reflect changes in feeding habits.

The presence of egg masses or paralarvae indicates regions where spawning occurs. Nigmatullin et al. (1995) report such occurrences from the tropical to subtropical regions of the Western Pacific Ocean, equatorial waters of the Indian Ocean near 80°E, off the tip of Brazil in the tropical western South Atlantic, the Mediterranean Sea, in the region of the Antilles in the tropical western North Atlantic, and off the coast of Peru in the eastern tropical Pacific Ocean. To these records we

add egg masses from the Atlantic off the southeastern coast of Florida, and the Bahama Islands and in the Pacific Ocean off Hawaii. Bower (2004) summarizes numerous records in the Pacific Ocean off southern Japan. With the exception of the Mediterranean Sea, spawning grounds appear to be world-wide in tropical waters. Specific patterns, if they exist, within this broad range have yet to be found.

### Juvenile

*T. rhombus* is best known as paralarvae or subadults. Juveniles are rarely caught in standard pelagic trawls. Young (1978) in his work on the vertical distribution of pelagic cephalopods off Hawaii captured no juvenile *T. rhombus* in midwater trawls even though paralarvae are commonly caught in plankton nets (e.g., Bower et al. 1999) and egg masses are occasionally seen (pers. obs., R. Young). Russian researchers using a variety of trawls up to 24 m mouth-width over a period of 20 years have captured 40 individuals from 10-100 mm ML (Nigmatullin and Arkhipkin 1998) which is the largest collection of juveniles known. The squid were captured in the upper 100 m but the time of capture was not reported. A 25 mm ML juvenile was caught in a trawl that fished between 55 m depth and the surface during the day (Roper and Young 1975). Nigmatullin and Arkhipkin (1998) suggest that juveniles between 15-50 mm ML occur at depths greater than 20-30 m during the day and night as they are rarely observed at night-light stations and are virtually absent from the diet of sea birds. Nigmatullin and Arkhipkin (1998) suggest that the juvenile phase ends at 120 mm ML when body shape and arm lengths (except arms III) are similar to subadults and suckers have 10-16 fang-like teeth on the distal margin and obtuse teeth on the proximal margin of the inner rings. See below for juvenile growth rates.

Juveniles, presumably, have the same geographical distribution as paralarvae.

### Subadult and Adult

#### *Age and Growth*

Nigmatullin et al. (1995) examined growth in *T. rhombus* based on statolith analysis of 72 individuals on the assumption that statolith increments were deposited daily. Ages ranged from 60 days (25 and 27 mm ML) to 309 days (770 mm ML); the largest squid examined, a mature male of 805 mm ML, had 288 increments. No apparent differences were noticed between male and female growth. Squid reached 90 mm ML at 90 days of age and 590 mm ML at 240 days. In juveniles growth rates were 1.2-1.5 mm per day but at an age of 150-180 days (ca. 275-400 mm ML) growth rates were exceptionally high at 4.6 mm day<sup>-1</sup> (ca. 140 mm mo<sup>-1</sup>). Bower (2004) reviewed studies of length-frequency data from the Sea of Japan that indicated growth rates of 80-100 mm mo<sup>-1</sup> for squid larger than 400 mm ML and he reported a tag-and-release study where one squid grew from 340-480 mm in 45 days (90 mm mo<sup>-1</sup>). At an age of 300 days, growth had slowed to 0.97 mm per day (ca. 30 mm mo<sup>-1</sup>) (Nigmatullin et al. 1995); their combined data set (males, females, juveniles) exhibited a logistic growth-curve when plotting ML or body weight (BW) against age in days. According to their curve of BW vs age, a squid will reach 10 kg at about 240 days old. Nigmatullin et al. (1995) suggest that maximum longevity is about 12 months and this is supported by the size-frequency data of Kawasaki and Kakuma (1998).

Kawasaki and Kauma (1998) reported on 13,876 squid caught by research and commercial fisheries around Okinawa from 1990-1994. The squid ranged in size from 300-900 mm ML. The 300-400 mm size group recruited into the fishery each year around June. The size mode increased to 600 mm by November and 700 mm in January and reached 750 mm in March. Growth rates ranged from 50-100 mm mo<sup>-1</sup> in the summer to 20 mm mo<sup>-1</sup> in March. These values are very close to those determined by Nigmatullin et al. (1995). Kato et al. (2001) suggest that the fast growth rates are related to relatively slow swimming; Kato, et al.'s ultrasonic tracking indicated that the squid did not swim against strong currents. (Undulatory swimming with fins is a slower but energetically more efficient means of locomotion than jet-swimming (Wells and O'Dor 1991)).

Kato et al. (2001) found gonad somatic indices (relationships between gonad and body weight) were maximal in March to May in Okinawan waters and egg masses were found in April. From January to May the sex ratio was approximately 1:1 but the percent of females dropped in June to August with a low of about 30% female in July. Kawasaki and Kakuma (1998) suggest that spawning in Okinawan waters occurs between January and September with a peak in March to May. Dates of hatching based on statolith increment counts from squid captured in the Pacific Ocean near the southern tip of Kyushu Japan (ca 5° of latitude north of Okinawa), indicate hatching occurred in all months except August, November and December (data summarized in Bower 2004) which agrees fairly well with spawning dates suggested by Kawasaki and Kakuma. Seasonal trends in hatching, if any, in more tropical waters have not been reported. In the Sea of Japan, Bower (2004) reports a study by Miyahara and Gorie (2003) in which squid that recruit into the fishery beginning in August grow faster than those recruiting after October.

According to Nigmatullin and Arkhipkin (1998) sex can be determined visually at a squid size of 100-120 mm ML and males mature between 390 and 450 mm ML; all males were mature beyond 450 mm ML (ca. 200 days old). Females mature between 520 and 650 mm ML; all females were mature beyond 650 mm ML (ca. 250 days old). Bower (2004) referring to Japanese research in the Sea of Japan quotes values of 470-520 mm ML for mature males and 590-610 mm ML for mature females. *T. rhombus* exhibits unusual sexual dimorphism in the length of arms III which, in immature males, can be twice as long as in females (Nigmatullin and Arkhipkin 1998). These authors suggest the long third arms aid in sexual recognition during pair formation; however, the bisexual nature of the pairs is questionable (Takeda and Tanda 1998).

### *Population Structure*

Kitaura et al. (1998) looked for genetic variation, between squid caught in the Sea of Japan, in the Western Pacific Ocean near Okinawa and the Ogasawara Islands, and in the Eastern Pacific Ocean near the Galapagos Islands, by sequencing deoxyribonucleic acids (DNA) of the mitochondrial cytochrome oxidase I gene. They found no evidence of genetic differentiation among squid from around Japan or between squid on both sides of the Pacific Ocean. This study suggests an absence of genetic differentiation but is not conclusive.

Kawasaki and Kakuma (1998) found a linkage between catch fluctuations in different regions around Okinawa which suggested to them that the catch represented changes in the local stock size.

Nishimura (1966) reported that fishermen generally found *T. rhombus* as a male/female pair and catch frequency in set nets supported the paired occurrence. Nigmatullin and Arkhipkin (1998) reported that *T. rhombus* observed from ships is usually seen as a pair of squid swimming together and suggest that the squid is monogamous, with male-female pairs remaining together from the juvenile stage to death. However, Takeda and Tanda (1998) suggest that fishermen in the Sea of Japan used an unreliable method for sexing squid and while the squid may normally occur in pairs these pairs are not always bisexual.

### *Horizontal Migration*

The only evidence of a horizontal migration for *T. rhombus* is the influx of squids into the Sea of Japan. Nishimura (1966) noted the common occurrence of *T. rhombus* along the western coasts of mostly middle and southern Honshu but occasionally as far north as Hokkaido. Records were based on beach strandings and captures in set nets near shore and other fishing methods offshore. Catches were mostly from mid-October to mid-January and disappeared after late January despite the continued presence of set nets. The squid appear in offshore waters just north of the Korean Straits (southwestern end of the Sea of Japan) from late August to mid-November and appear in November to January in the inshore waters of the same region as well as the inshore waters of middle Honshu. In addition, occasionally in the northern waters near the Tsugaru Straits (between Honshu and Hokkaido) *T. rhombus* is sometimes caught earlier in the season than in the more southern locations. These data suggest to Nishimura (1966) that the following migration occurs: (1) *T. rhombus*, like some warm-water species of fish and turtles, moves into the Sea of Japan on the Tsushima current through the Korean Straits during periods of peak transport from August to October and is distributed over most of its range in the open sea. (2) In mid-November when the northwest monsoon season begins, winds form onshore currents which carry the squid toward shore where much of the population is caught in set nets or stranded on beaches. (3) Surviving squid return to tropical waters following a southward current along the coast to the Korean Straits or some pass through the northern Tsugaru Straits with an unknown fate. The migration as envisioned by Nishimura could be largely passive with currents responsible for most transport. Nazumi (1975 cited in Bower 2004) suggested that this is a one-way migration and that *T. rhombus* dies in the cold water of the Sea of Japan during the winter. This latter conclusion has been accepted, until recently, by scientists reporting in the popular literature (Okutani 1982, Okiyama 1995 cited in Takeda and Tanda 1998). Takeda and Tanda (1998), however, found small squid (e.g., 156 mm ML) in December in the Sea of Japan, and they report that small sizes are caught off Kyoto in December. They suggest that the migration is not a simple one (a conclusion also reached by Nishimura in 1966) and the possibility exists that *T. rhombus* spawns and grows during the summer and autumn in the Sea of Japan.

### *Swimming Speed*

Like most muscular squids, *T. rhombus* is negatively buoyant and must swim to stay afloat (Nigmatullin and Arkhipkin 1998). Nigmatullin et al. (1995) report that the length of the statoliths in large *T. rhombus* is about half that of large oceanic ommastrephid squids. The significance of this is uncertain but could relate to fast acceleration. According to Nigmatullin and Arkhipkin (1998), however, *T. rhombus* is relatively inactive and is usually observed at night-light stations moving slowly with sinusoidal undulations of the large fins and with little contribution from their jet. Nishimura (1966) observing swimming *T. rhombus* in set nets also found they were slow

swimmers that swam mostly by movement of the fins. Nigmatullin and Arkhipkin (1998), however, note that *T. rhombus* is easily disturbed and reacts quickly with powerful escape jets that, in small squid (at least to 250 mm ML according to Nishimura 1966), can propel it from the water. Ultrasonic telemetry (of three squid 750-770 mm ML followed for 14 -72 hrs. off Okinawa) averaged about 2.0 km/hr (= 0.56 m sec<sup>-1</sup> or about 0.7 MLs sec<sup>-1</sup>), during both day and night (Yano et al. 2000). The range among the averages of the three squid was 1.76 km/hr (0.49 m sec<sup>-1</sup>) to 2.32 km/hr (0.64m sec<sup>-1</sup>). The maximum one hour average was 3.9 km/hr and the minimum about 0.2 km/hr. At 0.7 ML/sec (mantle lengths per second); their average speed is comparable to that of *Ommastrephes bartramii* which exhibits a far more active behavior around night-lights. Yano et al. (2000) mentions measurements made by Iizuka on swimming speeds of *T. rhombus* in the Sea of Japan by ultrasonic telemetry. The squids were smaller (480 and 490 mm ML) and the swimming speeds were 0.9-1.3 km/hr or 0.5-0.7 MLs sec<sup>-1</sup> which is comparable to the Okinawa measurements.

### *Spawning*

*T. rhombus*, based on circumstantial evidence, appears to be a “continuous spawner” with the following characteristics: continuous asynchronous ovulation and maturation of oocytes, spawning (i.e., monocyclic) over an extended period with intermittent spawning events (i.e., as the oviducts fill, they are emptied) and somatic growth during the period of spawning (Nigmatullin et al. 1995). These authors suggest that the number of oocytes that potentially will develop into mature eggs is fixed before maturation of oocytes begins. They estimate total potential fecundity from the number of oocytes at up to 4.8 million eggs. Nigmatullin and Arkhipkin (1998) suggest that individual spawning lasts 3-4 months and that a female will produce at least 8-12 egg masses during this period.

### *Vertical Distribution*

Takeda and Tanda (1998) reported on experimental fishing near Okinawa using standard commercial fishing methods involving a buoy and vertical drop-line but with jigs placed at specific depths during the day. Squid were caught between depths of 300 and 750 m with greater catches and CPUE between 400 and 650 m and slight peaks at 500 and 550 m. Temperatures at 750m were 5.8°C and at 500-550m temperatures ranged from 8.1 - 12.0°C. Depth records determined from biotelemetry by Yano et al. (2000), although somewhat inconsistent, showed the squid mostly at 300-550 m depth (considerable time was spent between 500-550m) during the daytime and from the surface to 150 m at night. Bower (2004) reports six other biotelemetry studies off Okinawa that confirm a day depth between 300-600m and a night depth at 0-150m. Yano et al. (2000) mention similar measurements made by Iizuka in the Sea of Japan where the squid occupied depths of 50-100 m during the day and 0-40 m at night (The Sea of Japan has a “false bottom” formed by extremely cold temperatures that can be less than 2° C at depths of 250 m (Anon. 2004)).

## Prey and Predators

### *Prey*

In the Sea of Japan *T. rhombus* has a very specialized diet. The review by Bower (2004) sites a study by Nazumi in 1975 on 52 adults which fed predominately on the adult ommastrephid squid *Todarodes pacificus* (frequency of occurrence was 89%) but also had sardine scales in 11% of the squid. Stomach contents of *T. rhombus* > 200 mm ML from Okinawan waters referred to by Bower (2004) stated that fishes were in 84% of the stomachs and squids in 38%. Squid from open ocean waters of the Eastern Tropical Pacific Ocean (ETPO) and Atlantic Oceans fed mostly on mesopelagic fish and squid (Nigmatullin and Arkhipkin 1998). In this latter study most prey were small: most of the fish were 30-100 mm in total length and squid were 30-120 mm in length (tip of mantle to tip of arms). Fish prey were mainly 6-8% of the squid length (not ML) except for long slender fish which were mainly 12-20% and squid prey were mainly 5-8%. Fish included *Cyclothone* (gonostomatidae), *Argyropelecus affinis* (Sternoptychidae), *Chauliodus sloani* (Chauliodontidae), *Paralepis* (Paralepididae), Myctophum, Diaphus, Hygophum (Myctophidae), *Nemichthes* (Nemichthyidae), *Beloniformes* juveniles, *Cubiceps* (Nomeidae), *Diplospinus* (Gempylidae), *Stomias* (Stomiatidae). Squid included *Abraliopsis* (Enoploteuthidae), *Octopoteuthis* (Octopoteuthidae), *Onychoteuthis banksii* (Onychoteuthidae), *Ctenopteryx* (Ctenopterygidae), *Histioteuthis* (Histioteuthidae), *Dosidicus gigas*, *Sthenoteuthis oualaniensis* (both young Ommastrephidae), *Liocranchia* (Cranchiidae), *Japetella diaphana* (Bolitaenidae) and *Ocythoe tuberculata* (Ocythoidea). Underwater observations by Nigmatullin in 1987 (Nigmatullin and Arkhipkin 1998) show that *T. rhombus* feeds at night but not actively. Nigmatullin and Arkhipkin (1998) concluded that this squid feeds mainly in the daytime in deep water.

### *Predators*

Nigmatullin and Arkhipkin (1998) found paralarvae and small juveniles of *T. rhombus* in the stomachs of several ommastrephid squids and a needlefish but in low frequency (<1-1.5%). They note that large juveniles of *T. rhombus* have been found in dolphin fish, lancet fish and various tunas generally in low frequency although in one study they occurred in 7.5% of bigeye tuna in the Gulf of Guinea. Young are rarely found in stomachs of sea birds. They report that large (>200 mm ML) *T. rhombus* are found in sharks, blue marlin, rough-toothed dolphins, spotted dolphins, false killer whales, sperm whales and swordfish. Hernandez-Garcia (1995) found frequencies of occurrence in swordfish of 0-11.8% in the eastern tropical Atlantic. Guerra et al. (1993) examined swordfish from the northeast Atlantic between 33° and 50° N but found no *T. rhombus* although *Sthenoteuthis pteropus* (similar Atlantic habitat to *T. rhombus*) was common. Seki (1993a) found *T. rhombus* remains in 7 of 22 swordfish examined in the subtropical central North Pacific Ocean. Markaida and Sosa-Nishizaki (1998) found *T. rhombus* in 15% of swordfish stomachs captured off Baja California but that they contributed only 1.5% of the prey by weight. Tsuchiya et al. (1998 cited in Bower 2004) found *T. rhombus* comprised 10% of the prey items of the swordfish in the tropical Eastern Pacific Ocean and 3% in both yellowfin and bigeye tunas.

### Habitat

The general geographical distribution of *T. rhombus* was reviewed by Nigmatullin and Arkhipkin (1998). The species range includes the tropical and subtropical regions of the world's oceans and

extends into warm temperate regions of the Mediterranean Sea, the Sea of Japan in summer, and off South Africa: (1) In the Atlantic the range extends to 30-40° north and south near the continents where western boundary currents carry warm waters into high latitudes. (2) In the central regions of the Atlantic *T. rhombus* occurs up to 20°N and 25°S. (3) In the Southeast Atlantic it reaches only 18°S due to the cold waters of the Benguela Current. (4) In marginal seas of the Atlantic, it is present in the Gulf of Mexico, Caribbean and Mediterranean Seas. (5) In the Indian Ocean it is known from the Arabian Sea and gulf of Bengal and up to 35°S off the tip of South Africa along with the warm Agulhas Current. (6) In the Western Pacific Ocean it is found from the Sea of Japan at 43°N to 25°S. (7) In the Western Pacific Ocean it reaches about 20° north and south. *T. rhombus* occupies waters primarily where surface temperatures are more than 20°C although it is known from SSTs of 15°C. A more detailed indication of the latitudinal boundaries in the central North Pacific Ocean is found in the reports of the by-catch of the drift-net fisheries: Seki (NMFS unpublished) reports pooled catches by large-mesh driftnets that show scattered catches of *T. rhombus* with northern-most catches at approximately 38.5°N at 170 °E and further west at 35°-36°N at 149° - 163°E and eastward at 32°N at 158°W.

The vertical extent of the habitat extends from the surface to at least 600 m depth in oceanic waters.

#### Status of the Stock

Genetic data have, so far, failed to distinguish populations of *T. rhombus* across the North Pacific Ocean (see above) and morphological data have failed to distinguish populations world-wide (Nigmatullin and Arkhipkin 1998). Some data (see above) from the Okinawa fishery suggest that catches are from a resident population. In most areas, however, little data exist on how mobile populations are.

The fishery off Okinawa, which started in 1989 and uses drop-line and long-line fishing methods, catches about 1600-2000 mt yr<sup>-1</sup> (Kato et al. 2001). The total Japanese fishery yield of *T. rhombus* was nearly 6000 mt in 2001 (Bower 2004). Experimental fishing in the South China Sea produced almost no results (Dickson et al. 2000).

Nigmatullin and Arkhipkin (1998), based on night-light observations and trawl catches, report an estimate of 1.5-2.5 million tons world-wide. This “educated guess” is, apparently, the only estimate that exists.

### **Purpleback Flying Squid (*Sthenoteuthis oualaniensis*)**

#### General Description

*Sthenoteuthis oualaniensis*, commonly known as tobiika, hoyenjoo, yellow-backed squid, purpleback flying squid, flying squid and purple squid, is a member of the family Ommastrephidae and thought to be the most abundant large squid in the tropical and subtropical waters of the Indo-Pacific region (Young and Hirota 1998, Dunning 1998). A related species, *Sthenoteuthis pteropus*, the only other member of the genus, replaces *S. oualaniensis* in the Atlantic Ocean.

*S. oualaniensis* consists of five possible forms (see Section 3.4.3.4.2 Population Structure). This report is restricted primarily to the dominant form in the Pacific Ocean: the late-maturing medium form. We use the name, *S. oualaniensis*, to refer to this form; references to other forms will be made by using their form name. Unless indicated otherwise, data are taken only from Pacific Ocean populations.

Although abundant, concentrations of the squid are usually insufficient to support major fisheries. Local fisheries, however, have existed off Taiwan, the Ryukyu chain (Okutani and Tung 1978) and Hawaii (Yuen 1979).

In Hawaiian waters, *S. oualaniensis* females mature between 158 and 205 mm ML with 90 percent mature at 200 mm ML (maximum size is 335 mm ML, 1.6kg); males are mostly mature by 140 mm ML (maximum size is 210 mm ML) (Young and Hirota 1998, Suzuki et al. 1986). The length/weight relationship for females in Hawaiian waters is given by  $W=(1.8 \times 10^{-5})L^{3.15}$  with L (length) in mm and W (weight) in g and the curve for males is essentially the same (Suzuki et al. 1986). The life span of *S. oualaniensis* is estimated to be about one year.

*Sthenoteuthis* is an obligate shoaling animal (numbering 2 to 1000 individuals) and, at low squid densities, it forms shoals of different sizes and Occasionally will attempt to join fish shoals (Zuev et al. 2002).

#### Eggs and Paralarvae

An egg mass from a Pacific Ocean member of *S. oualaniensis* has never been seen. An egg mass, spawned in captivity, by the giant form of *S. oualaniensis* from the Arabian Sea, however, has been reported to have the “typical ommastrephid” appearance (Chesalin and Giragosov 1993). This means a large spherical, gelatinous egg mass with thousands of eggs distributed throughout the mass. Mature oocytes (eggs) are small; those in the oviduct measure 0.79 x 0.87 mm (Okutani and Tung 1978) or 0.70 x 0.84 mm, (Sakurai et al. 1995).

The vertical distribution of paralarvae appears to be mostly the upper 50 m or so of the ocean during both the day and night. In Hawaiian waters Young and Hirota (1998) found 60-70 percent of the paralarvae in the upper 20 m during both the day and night with small numbers found to depths of 81-100 m. Harman and Young (1985), off Oahu, Hawaii, found most paralarvae in the upper 70 m in April and the upper 50 m in October, with some captures as deep as at least 150 m. Saito and Kubodera (1993), south of Japan, found paralarvae mostly in the upper 40 m, although over the continental shelf in the East China Sea they caught paralarvae between 30 m and about 60 m.

Harman and Young (1985) found that paralarvae were present throughout the year in Hawaiian waters but were most abundant in August, less abundant in April and least abundant in October and December. Some seasonal overlap occurs between the occurrence of paralarvae of *S. oualaniensis* and the related *Ommastrephes bartramii* in Hawaiian waters. Off leeward Oahu, *O. bartramii* was not collected by Harman and Young (1985). Young and Hirota (1990), however, found both species at this same site and in the same month (April) in a subsequent year. Apparently during the 1985 study either *O. bartramii* had a more abbreviated spawning period or they did not spawn as far south as in the later study (Young and Hirota 1990). Bower et al. (1999)



found that *O. bartramii* paralarvae were more abundant than *S. oualaniensis* paralarvae in northern Hawaiian waters in the winter by over a 12:1 ratio and that *S. oualaniensis* paralarvae were more “island associated.” These data suggest that much of the spawning of these two species is out of phase with one another in time and space over much of the year in these waters. Saito and Kubodera (1993) found a similar inverse spatial relationship of *S. oualaniensis* and *O. bartramii* paralarvae in the western Pacific Ocean. The former was over ten times more abundant in Saito and Kubodera's southern transect to the south of Japan and the latter was about three times more abundant in the northern transect off Tokyo.

*S. oualaniensis* paralarvae have only been positively identified since 1985 (Harman and Young 1985) so some earlier records may be unreliable. Paralarvae in the Pacific Ocean are known from Hawaiian waters (Harman and Young 1985, Young and Hirota 1998, Bower et al. 1999), Japan and Taiwan (Okutani and Tung 1978); off Japan at about 34°N (water temperature 25-26°C) and a transect across the Amami-Ryukyu Islands into the East China Sea (water temperatures 21-31°C) (Saito and Kubodera 1993), ETPO (Yatsu 1999). Dunning (1998) reports paralarvae between 14° and 34°S off the eastern Australian coast where temperatures range from 20.4°-28°C in the summer. He found paralarvae rare from January to May 1983 in the region from 28°-34°S and absent from this same area in the summer of 1985. An assumption that spawning occurs throughout the habitat of *S. oualaniensis* (except, perhaps, at the high latitude extremes of their distribution) is unwarranted considering the sparsity of data and the evidence that marked patterns in the distribution of mature females can occur on rather small scales. Indeed, in the Atlantic Ocean *Sthenoteuthis pteropus* spawns primarily in specific regions on either side of the tropical Atlantic (Zuev and Nikolsky 1993).

Bigelow (1991) examined growth of paralarvae based on statolith increments of 6 paralarvae and derived a growth curve of  $ML=1.46e^{0.034x}$ , where ML is in mm and x is in days. This curve indicates a paralarva of 4 mm ML is 30 days old which is in strong contrast to the growth of *O. bartramii* which reaches 7 mm ML at 30 days. Arkhipkin and Mikheev (1992) in a detailed study of *S. oualaniensis*'s larger congener, *S. pteropus* from the tropical Atlantic, found paralarval growth comparable to that of *O. bartramii*. Proboscis separation in *S. pteropus* occurred at a ML of 8.5 mm and an age of 33-35 days. Presumably the Bigelow study examined too few specimens to obtain a reliable curve, but emphasizes the probable large variation that exists in growth rates of paralarvae.

Harman and Young (1985) found that the morphological event separation of the tentacles, usually thought to mark the end of the paralarval period in ommastrephids, occurred at about 9 mm ML in *S. oualaniensis*. The validity of this event as the marker, however, has been questioned by Yatsu and Mori (2000).

### Juvenile

Little direct evidence exists on the geographical distribution of juveniles although Dunning (1998) was successful in capturing juveniles with scoop nets between 22°50'S and 38°25'S where SSTs were 26.7°-20.8°C. According to Okutani juveniles are frequently aggregated in inshore waters around oceanic islands such as Hachijo Island and Ogasawara Islands (Bonin Islands), Seychelles in the Indian Ocean and Guadalupe Island, Mexico (Okutani and Tung 1978).

The vertical distribution of juveniles is also poorly known. Presumably they occupy near-surface waters during the day and night. Small *S. oualaniensis* have been found to glide onboard ship during the day (Young and Hirota 1998). Small *Sthenoteuthis* have been observed gliding over the surface of the ocean during the day (Arata 1954, Young 1975, Okutani and Tung 1978) and are commonly found in the stomachs of day feeding birds (Ashmole and Ashmole 1967). They are also encountered at the surface at night (Young and Hirota 1998).

The features that mark the end of the juvenile period in *S. oualaniensis* have never been clearly defined. *S. oualaniensis*, however, has a diagnostic photophore patch on the anterodorsal surface of the mantle. The dorsal photophore patch becomes apparent at approximately 100 mm ML (Kishimoto and Kohno 1992, Nesis 1993). The presence of the photophore patch can be taken as a working marker for the end of the juvenile phase and the beginning of the subadult phase. The hectocotylus develops at about 110 mm ML (Okutani and Tung 1978). In the study by Arkhipkin and Mikheev (1992) on the age of *S. pteropus*, based on statolith examination, they recognized a “dark zone” in the statolith characterized by the lower transparency of the statolith and the width of the increments. They found that this period ended at about 100-110 days at a ML of about 100 mm which they considered to be the end of the juvenile period for *S. pteropus*.

### Subadult and Adult

#### *Age and Growth*

Russian research, reviewed by Nesis (1993), indicates males of *S. oualaniensis* reach 15-17 mm in 6-7 months and are thought to live less than a year. The growth rates, determined by growth marks on statoliths and gladii, of the middle and dwarf forms are nearly the same, but the life span is short in the small forms, probably not more than 6 months. Gross growth efficiency (weight of growth divided by the weight of food eaten) is estimated at 10 percent throughout the postparalarval life.

Yatsu (2000) determined growth curves for both male and female *S. oualaniensis* based on statolith increments from about 120 mm ML to about 290 mm ML for females and about 185 mm ML for males. His curves are:  $ML=9.9511X^{0.634}$  (females) and  $ML=29.9X^{0.3494}$  (males) with ML in mm and x in days (presumably). According to this curve a female of 120 mm ML is 51 days old. This contrasts strongly with data of Zaidi bin Zakaria (2000), which places a 115 mm ML female at an age of 95 days. Because ommastrephid growth is affected by food availability and ambient temperature, growth rates can vary with season, geographic area and year (Yatsu 2000). The data of Zaidi bin Zakaria came from the South China Sea west of the Philippines but, unfortunately, Yatsu (2000) didn't state the locality from which his data were obtained.

In Hawaiian waters *S. oualaniensis* females mature between 158 and 205 mm ML with 50 percent mature at 166-175 mm ML and 90 percent mature at 200 mm ML (maximum size is 335 mm ML); males are mostly mature by 140 mm ML (maximum size is 210 mm ML) (Young and Hirota 1998, Suzuki et al. 1986). In northern Australian waters males reached maturity from 160 mm ML and females from 250 mm ML. In the ETPO, Nesis (1977 in Dunning 1998) found males mature over 110 mm ML and females at 180-190 mm ML.

### *Population Structure*

Nesis (1993) has described a complex population structure for *S. oualaniensis* that incorporates three major and two minor forms. A giant form that occurs only in the northern Indian Ocean in the region of the Red Sea, Gulf of Aden and Arabian Sea (modal sizes of 400-500 mm ML in the Arabian Sea, maximum size of 650 mm ML), a medium form (modal sizes of 120-150 mm for mature males and 190-250 mm for mature females) that occurs throughout the range of the species and a dwarf form (modal size of 90-100 mm ML for mature males and 90-120 mm ML for mature females, 140-150 mm ML maximum) that occurs in equatorial waters and lacks the dorsal mantle photophore patch characteristic of the species. The medium form may be subdivided into two forms based on features of the gladius (double or single lateral axes of the rhachis). One of the two medium forms (single lateral axes of the rhachis) occurs only in the Red Sea, the Gulf of Aden and the Arabian Sea north of 15°-17°N. Complicating this picture is a small form, similar to the medium form but maturing at a smaller size (mode for females is 120-140 mm with a range of 90-160 mm ML) that is nearly the same size as the dwarf form and is found in the Western Indian Ocean and the ETPO. Of the five possible forms, giant, medium with single axis, medium with double axis (the typical *S. oualaniensis*), small and dwarf, the latter three occur in the Pacific Ocean. The dwarf equatorial form is found roughly within 10° latitude of the equator where it co-occurs with the typical *S. oualaniensis*.

The dwarf form has several morphological characters that separate it from the typical *S. oualaniensis* (absence of the dorsal photophore patch, slightly different hectocotylus and slight differences in the spermatophore structure and in the gladius structure [Nesis 1993]). Nesis (1993) could find no differences in the appearance of paralarvae between the dwarf and middle forms. Researchers have disagreed on whether or not the dwarf form is a distinct species (Clarke 1966, Wormuth 1976, Nesis 1993). The most recent research on the status of the dwarf form has been done by M. Roeleveld-Companyo and she considers it to be a separate species that can only be identified as an adult. In Hawaiian waters only the typical *S. oualaniensis* is present. Snyder (1998) suggests that the giant form results from a plastic phenotype in the species.

On a more local scale, Okutani and Tung (1978) found *S. oualaniensis* in Taiwanese waters to consist of three different seasonal cohorts: a June-spawning group, a September-October spawning group and a February-March spawning group.

### *Horizontal Migration*

*S. oualaniensis* does not undergo horizontal migrations like *O. bartramii* although the high-latitude limits of the population may change seasonally. *S. oualaniensis*, however, does exhibit small-scale areal patterns in the vicinity of islands. Around the Hawaiian Islands large mature females are located on the windward (northeastern) sides of the islands, small immature females are located primarily within 25 kilometers (km) of the leeward (southwestern) sides of the islands and somewhat larger mostly immature females are found mainly further offshore on the leeward sides of the islands (Young and Hirota 1998). The reason for these patterns is unknown but Young and Hirota (1998) found some differences in feeding patterns between windward and leeward areas. These local patterns and those observed in juveniles (Okutani and Tung 1978) and in paralarvae (Bower et al. 1999) support a general occurrence for island-related distribution patterns.

Nesis (1993) found that the sex ratio is nearly equal among young squids but strongly shifted to females among subadults/adults, which he attributed, apparently incorrectly, to the shorter lifetime of males. In Hawaiian waters among all squid captured larger than 100 mm ML females exceed males in abundance by a 3:1 ratio (Young and Hirota 1998). At 140-150 mm ML (the size of peak abundance of males) the ratio of females to males was about 1.6:1. The shape of the size-frequency curves of all squids caught suggests that the sexes are about equally abundant until about 130 mm ML when males start to mature. This sex ratio is in strong contrast to that found for adult *Ommastrephes bartramii* captured in Hawaiian waters, where the female to male ratio was 1:8 (Young et al. 1997). Young and Hirota (1998) after examining several alternatives concluded that the reason for the predominance of females in the catches was unresolved. Okutani and Tung (1978) report a similar situation off Taiwan and Okinawa. The sex ratio is 1:1 at 100-130 mm ML while the relative abundance of males decreases beyond 140 mm ML. The average commercial catch favors females by a 3:1 ratio. In the Philippines the ratio of females to males caught by jigging machines was 4:1 (Siriraksophon and Nakamura 2001).

### *Swimming Speed*

There is no information available on swimming speed for this species.

### *Spawning*

*S. oualaniensis*, based on strong circumstantial evidence, is a “continuous spawner” (Harman et al. 1989, Young and Hirota, 1998, Rocha et al. 2001) with continuous asynchronous ovulation, ovulation during the spawning period, monocyclic maturation of oocytes, spawning over an extended period where spawning is intermittent but spawning events are continuous (i.e., as the oviducts fill, they are emptied) and somatic growth during the period of spawning. The batch fecundity of a female about 300 mm ML is 250,000 eggs in the combined oviducts (Harman et al. 1989). The number of oocytes in various stages of development in a female of 251 mm ML was estimated to be 1,643,000 (Harman et al. 1989). The length of the spawning period and the frequency of spawning episodes during this period are unknown.

### *Vertical Distribution*

At night squids are commonly observed from ships in surface waters. Young and Hirota (1998) suggest, based on the near absence of *S. oualaniensis* subadults/adults at night over bottom depths of less than 650 m, that this squid descends to at least 650 m during the day in Hawaiian waters where water temperatures would be around 4°-5°C. Dunning (1998) caught adult *S. oualaniensis* in eastern Australian waters only where bottom depths exceeded 600 m. In deep water, however, oxygen concentrations can be very low, which should prohibit a highly active squid from entering there.

*S. oualaniensis* has a very high metabolic rate (standard metabolism of 348 ml O<sub>2</sub>/kg/hr) that exceeds that of most fast-swimming oceanic fishes (Zuev et al. 2002). Its energy metabolism, as in other squids, is based mostly on protein; however, during metabolism a considerable proportion of the protein is catabolized anaerobically (Shulman et al. 2002). In this sense, these squid may be “preadapted” for low oxygen environments. In the Indian Ocean *S. oualaniensis* occupies depths

of 300-400 m during the day where the oxygen concentration is 0.1-0.2 mg/L (2-4% of saturation) (Shulman et al. 2002).

### Prey and Predators

#### *Prey*

The high metabolic rate and fast growth rates of *S. oualaniensis* indicate a high rate of food intake is required. Shulman et al. (2002) estimate that adult *S. oualaniensis* require a very high 8-10% body weight as a daily ration.

Schetinnikov (1992), in one of the most detailed feeding studies of *S. oualaniensis*, examined squids attracted by night-lights in the ETPO. He found that *S. oualaniensis* fed heavily on crustaceans (up to 50 percent of the volume of the diet) and fish larvae between 40 and 100 mm ML. Between 100 and 150 mm ML the proportion of crustaceans decreased greatly and crustaceans were largely absent at larger sizes. Beyond 150 mm ML myctophids dominated the diet but, as size increased, squids became progressively more important in the diet and by 300 mm ML squids comprised about 40 percent of the diet.

Local variation in the stomach contents of *S. oualaniensis* has been reported near oceanic islands. Squid captured southwest of Taiwan contained mostly fish, those taken east of Taiwan contained a mixture of fish and squid and around Okinawa they frequently contained crustaceans (Okutani and Tung 1978). In contrast to a nearly exclusively fish and squid diet in other areas around the Islands (Parry 2003), mature females captured off the northeastern coast of the island of Hawaii ate mainly crustaceans (Taguchi et al. 1985).

Okutani and Tung (1978) found that the stomach weight (relative to body weight) was higher in the first half of the night. Apparently the primary feeding period of subadults and adults follows their arrival in near-surface waters at night.

Among the 302 specimens of *S. oualaniensis* examined by Parry (2003) in Hawaiian waters, fish and squid comprised virtually the entire diet with fish being more abundant than squid. Stomach contents were analyzed by identifying fish otoliths and squid beaks contained in the stomachs. Among squids, enoploteuthids comprised 17 percent of the diet. Parry (2003) found that while *S. oualaniensis* fed on a subset of the broad diet of adult *O. bartramii* captured in the same waters and that myctophids were the most abundant items in both diets, *S. oualaniensis* is a more specialized predator than *O. bartramii*. For example, *Symbolophorus evermanni* comprised 7.5 percent of the stomach otoliths in *O. bartramii* but 37 percent in *S. oualaniensis*. Even when feeding on the same species of fish, differences in the size of the prey were apparent. Parry concluded that competition between the two squids in Hawaiian waters was low. Parry (2003) examined  $\delta^{15}\text{N}$  values of *S. oualaniensis* mantle muscle and found that values slowly increased in an exponential fashion with mantle length of the squid from paralarvae at 6.2‰ to about 8.2‰ in the larger squid. The curve is  $\delta^{15}\text{N}=4.208+1.873*1.0037^{\text{ML}}$  where ML is in mm, however considerable variability was present. The  $\delta^{15}\text{N}$  values suggest that *S. oualaniensis* occupies a lower trophic level than *O. bartramii* and supports the conclusion that competition between them is low.

## *Predators*

The distribution of *S. oualaniensis* overlaps with some of its larger close relatives in the same subfamily (Ommastrephinae), *Ommastrephes bartramii* at the high latitudinal end of *S. oualaniensis*'s distribution and *Dosidicus gigas* in the eastern tropical Pacific Ocean. Schetinnikov (1992) in examining the feeding habits of *S. oualaniensis* in the southeastern Pacific Ocean found that large *S. oualaniensis* would consume other species of squid up to 40 percent of its own mantle length and, in one region studied, fed heavily on young *Dosidicus gigas*. This predator/prey size-relationship suggests that, where their distributions overlap, adult *Ommastrephes bartramii* and *Dosidicus gigas* could be important predators on *S. oualaniensis*. In Parry's (2003) examination of the stomach contents of *S. oualaniensis* and *O. bartramii* he found no evidence for prey/predator interaction between the two species even though he commonly caught both species at the same station. His study dealt almost exclusively with mature *O. bartramii* and possible interaction among paralarvae and juveniles of both species is unknown, although their primary periods of spawning in Hawaiian waters appear to be somewhat out of phase seasonally and spatially.

A variety of studies indicate the presence of *S. oualaniensis* in the stomach of various predators. For example: *S. oualaniensis* made up 0.5 percent of the food items in the stomach and 8.6 percent of the weight (fifth most important) of prey of *Stenella attenuata* near Taiwan (Wang et al. 2003) with the average size of *S. oualaniensis* being 210 mm ML; *S. oualaniensis* comprised 11.5 percent by weight of the diet of the dolphinfish, *Coryphaena hippurus* in the ETPO (Olson and Galvan-Magana 2002); off Baja California, *S. oualaniensis* dominated the food of the swordfish in four of eight studies (Markaida and Sosa-Nishizaki 1998); *S. oualaniensis* made up 26 percent by weight of the diet of the pigmy sperm whale (*Kogia breviceps*) and 2.2 percent (by weight) of the diet of the dwarf sperm whale (*Kogia sima*) off Taiwan (Wang et al. 2003); Ashmole and Ashmole (1967) found *S. oualaniensis* in 34-97 percent of the birds examined at Christmas Island (Central Equatorial Pacific Ocean); Harrison et al. (1983) also found juvenile ommastrephid squid (frequently identifiable as *S. oualaniensis*) a common item in the diet of seabirds in the Northwest Hawaiian Islands but somewhat less so than at Christmas Island; Young (1975) reported skipjack tuna, yellowfin tuna, wahoo, probably bigeye tuna, the sooty tern and brown noddy as predators; Wormuth (1976) mentions the snake mackerel, *Gemplus serpens*, among other predators.

Although the evidence is still sketchy, *S. oualaniensis* is probably important in the diet of many, if not most, large fishes, marine mammals and many sea birds that forage within its habitat.

## Habitat

*S. oualaniensis* is a tropical IndoPacific species that occurs in the Pacific Ocean from southern Japan to southern Queensland and from just south of Baja California to northern Chile (Nesis 1987). Dunning (1998) records *S. oualaniensis* as far south as 38°40'S (SST 20.7°C) at the northern edge of the Bass Straits, near the coast of Australia. In the Coral Sea Basin (east of 155°E), however, adults were caught only north of 32°S (SSTs>23.5°C). Eastward from the Coral Sea to near the coast of South America Wormuth (1976) records its presence roughly along 20°S to about 110°W then his southern records reach about 15°S but stop about 4° of longitude west of Peru apparently at the edge of the Peru current. In the region of the Hawaiian Archipelago, *S.*

*oualaniensis* did not occur in winter north of 28°N. Between 23°N and 28°N large females were few and of those few most were not mature; the ratio of mature to immature females of squid 200 mm ML or larger was 1:27 during one cruise (Young and Hirota 1998). This suggests that at the northern end of their range, the females are not maturing normally. Tung et al. (1973) states that Taiwan (which lies roughly between 22 and 25°N) is at “the edge area of the migration sphere of the common squid [*S. oualaniensis*] in the southwest water of Taiwan... .” *S. oualaniensis* is recorded off Southern Japan at nearly 35°N (SST 25-26°C) (Saito and Kubodera 1993). Wormuth (1976) recorded the northern limit of distribution at 33.6°N and 165.5°E (September) and about 31°N at 156°W, 139°W and 129°W off Southern California west of the California Current. During the change of seasons the SSTs across most of the Pacific Ocean undergo a dramatic north-south movement. For example, north of Hawaii the 18°C isotherm can move from near 30°N in February to over 40°N in August (Lauritsen and Lynn 1991). The extent to which the latitudinal limits of the distribution of *S. oualaniensis* change with season are not known but do not appear to be very dramatic.

### Status of the Stock

*S. oualaniensis* has been commercially fished off Okinawa (in the Ryukyu chain), Taiwan and Hawaii. Fishing grounds existed on the southwestern coasts of Taiwan and beyond the 200 m bottom isobath of the Ryukyu chain (Okutani and Tung 1978). The fishing season in Taiwan is from March to November with a peak in May-August. Fishing was most productive at SSTs of 26°-28°C. The annual landings of squid and cuttlefish in Taiwan and Okinawa from 1947-1969 averaged 325 tons with 70 percent being *S. oualaniensis* (Okutani and Tung 1978). The *S. oualaniensis* catch is used for tuna bait and for human consumption (Okutani and Tung 1978). According to Lu (personal communication, 2003) the fishery never was very successful as the squid had low value for human consumption relative to other squid, due to its toughness. He states that at present there is no longer a targeted fishery for *S. oualaniensis* but fishers still take incidental catches of the squid. In Hawaii the fishery began with immigrants from Okinawa that fished off Hilo at night in small boats with handlines; however, it soon became apparent that they could also catch tuna and quickly tuna became the target of the fishery with squid being used as bait for the tuna or as incidental catch (Yuen 1979). This nighttime handline fishery has become known as the *ika-shibi* (squid-tuna) fishery. Between 1973 and 1975 the annual squid catch varied between 0.5 and 5.0 tons (Yuen 1979). Between 1976 and 1992 the annual squid landings in Hawaii varied from about 1-12 tons with large year-to-year fluctuations and no clear trends (HDAR unpub. data).

The biomass of *S. oualaniensis* standing stock in the South China Sea Area III (west of the Philippines) was estimated from jigging surveys at 283,000 metric tons (Labe 2000).

Zuev et al. (2002) estimated, based mostly on visual survey methods, the total instantaneous stock size of *S. oualaniensis* at 3-4 million tons (1.9-2.4 million tons for the middle-sized form) and an annual production to biomass ratio for adult squids of 8.0-8.5.