Aspects of the Natural History of Pelagic Cephalopods of the Hawaiian Mesopelagic-Boundary Region[1]

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ABSTRACT: Pelagic cephalopods of the mesopelagic-boundary region in Hawai'i have proven difficult to sample but seem to occupy a variety of habitats within this zone. *Abralia trigonura* Berry inhabits the zone only as adults; *A. astrosticta* Berry may inhabit the inner boundary zone, and *Pterygioteuthis giardi* Fischer appears to be a facultative inhabitant. Three other mesopelagic species, *Liocranchia reinhardti* (Steenstrup), *Chiroteuthis imperator* Chun, and *Iridoteuthis iris* (Berry), are probable inhabitants; the latter two are suspected to be nonvertical migrants. The mesopelagic-boundary region also contains a variety of other pelagic cephalopods. Some are transients, common species of the mesopelagic zone in offshore waters such as *Abraliopsis* spp., neritic species such as *Euprymna scolopes* Berry, and oceanic epipelagic species such as *Tremoctopus violaceus* Chiaie and *Argonauta argo* Linnaeus. Others are apparently permanent but either epipelagic (*Onychoteuthis* sp. C) or demersal (*Nototodarus hawaiiensis* [Berry] and *Haliphron atlanticus* Steenstrup). Submersible observations show that *Nototodarus hawaiiensis* commonly "sits" on the bottom and *Haliphron atlanticus* broods its young in the manner of some pelagic octopods.

THE CONCEPT OF the mesopelagic-boundary region (m-b region) was first introduced by Reid et al. (1991), although a general association of various mesopelagic animals with land masses has been known for some time. They defined the horizontal and vertical limits of the daytime zone in Hawai'i waters as depths of 400–700 m that occur above bottom depths of the same range. Recently S. B. Reid (unpubl. data) has found that the zone is more extensive than originally thought; the m-b region now includes the former boundary region, now termed the "outer mesopelagic-boundary zone" (outer m-b zone), and a new zone, the "inner mesopelagic-boundary zone" (inner m-b zone). The latter is defined as depths of ca. 250–400 m that lie over bottom depths of the same range. The designation of an inner zone is based on Reid's finding mesopelagic fishes resident there during both the day and night; mesopelagic fishes are virtually absent at these daytime depths in waters seaward of the boundary zone. At least two species of boundary animals in Japan, the squid *Watasenia scintillans* (Berry), and the shrimp *Sergia lucens* (Hansen), undergo daily horizontal migrations toward and away from shore (Sasaki 1914, Omori and Ohta 1981). Reid (unpubl. data) found some evidence for similar migrations in Hawaiian boundary lanternfishes (myctophids).

Knowledge of the species composition, distribution, and movements of the pelagic fauna of the boundary region in general is poor, and for cephalopods it is almost nonexistent. This paper reports on the cephalopods taken during an extensive sampling program in Hawaiian waters and draws on data from other studies in this region to summarize our present understanding of the boundary region's cephalopod fauna.

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TABLE 1

SUMMARY OF TRAWLING EFFORT BY THE THREE PROGRAMS

PARAMETER	UH: IKMT	UH: NEUSTON	NMFS	Hokusei Maru
Net mouth, m^2	40	1.6	100	200
Time	Mostly night	Night	Night	Twilight-night
Maximum depth	Mostly 200 m	Surface	147 m	250 m
Tow duration	1.5 hr	1.5 hr	2 hr	2 hr
Inner m-b tows	163	142	2 +	0
Outer m-b tows	147	171	2 −	7

MATERIALS AND METHODS

Most squids were captured during three trawling programs: (1) A series of seven tows taken from the *FTS Hokusei Maru* (HM) with a commercial-size net having a mouth opening of ca. 200 m^2 (graded mesh, 400 mm to 14 mm stretch). These tows fished from 250 to 0 m at a speed of ca. 1.5 cm/sec during twilight from 1800 hours to 2000 hours local time. Data from the HM tows and incidental data taken with either a 8-m^2 mouth Isaacs-Kidd (IK) trawl or a 40-m^2 mouth rectangular trawl have been reported previously (Reid et al. 1991). All of the HM tows were taken in the outer m-b zone. (2) A series of four tows taken from the *R/V Townsend Cromwell*, National Marine Fisheries Service (NMFS), with a pelagic rope trawl with a 100-m^2 mouth (graded mesh, 292 mm to 19 mm stretch). These were open stratified oblique tows to a maximum depth of 147 m that fished primarily between 50 and 100 m. Two of these tows, taken off leeward O'ahu, fished parallel to the coast along a steep slope. Bottom depths there drop from 100 to 400 m over a horizontal distance of about 1 km. Two tows, taken off windward O'ahu, fished orthogonal to the coast over bottom depths of ca. 100–1000 m. Therefore, two tows fished the inner m-b zone, and two tows passed through the inner and outer m-b zones and terminated in more oceanic waters. (3) A series of 633 tows taken from the *R/V Moana Wave*, University of Hawai'i (UH series), approximately evenly split between those with a 7-m IK with a 40-m^2 mouth (graded mesh, 200 to 3 mm stretch) and a 2-m neuston trawl with an effective mouth area of 1.6 m^2. All sampling involved the use of open nets, and most tows were taken at night. S. B. Reid will provide details of the UH sampling program in a forthcoming paper. Most IK samples in that series were oblique tows from 0 to 200 m, but shallower tows (0 to 50–75 m) were necessary when bottom depth was 100 m and at the edge of Penguin Bank (0–100 m), where shallow pinnacles made standard trawling hazardous. A few horizontal and daytime tows were also taken. We sampled during regular time periods during the night and just before sunset and after sunrise. Most tows were taken over bottom depths of 700 m or less and at speeds of 1.75–2.0 m/sec. The number of tows was approximately evenly split between the inner m-b zone and the outer m-b zone. Neuston tows were taken concurrently with the IK samples. The trawling data are summarized in Table 1. In addition to trawling, visual observations and video recordings of boundary animals were made during three dives with the University of Hawai'i submersible *Pisces V* during the daytime off leeward Lāna'i over bottom depths of 250–600 m.

RESULTS

Abralia trigonura Berry

The largest catches of *A. trigonura* were made by the large HM trawl. The maximum catch was 787 squid, and catches exceeded 100 individuals in all seven tows (Reid et al. 1991). Measurements were made from a representative sample of 1439 *A. trigonura* taken by HM trawls; of these 45% were mature
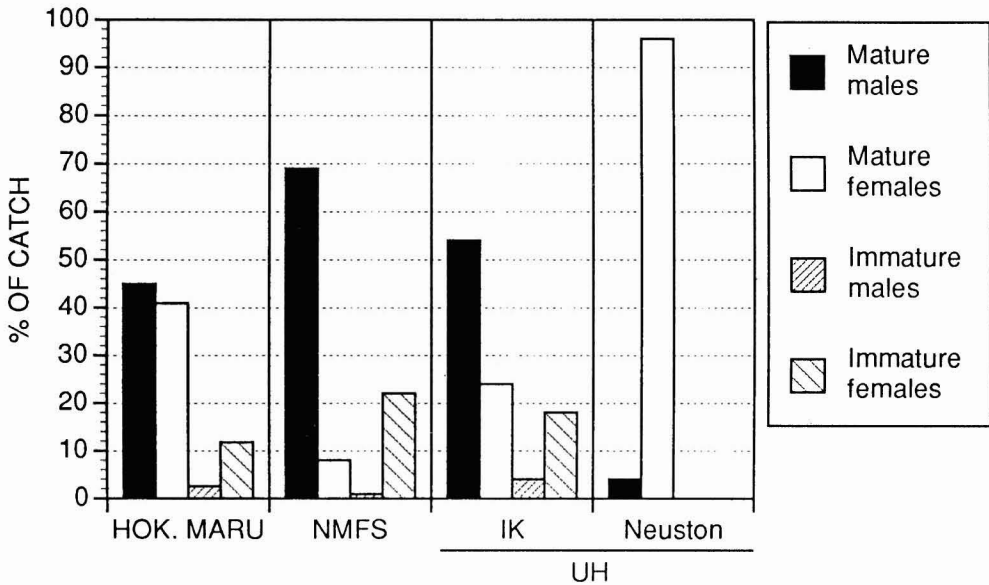
FIGURE 1. Comparison of catches of various stages of *Abralia trigonura* from the different sampling programs and different trawls. HOK. MARU, *Hokusei Maru* 200-m² trawl; NMFS, National Marine Fisheries Service 100-m² rope trawl; UH, University of Hawai'i, IK, 40-m² trawl, Neuston, 1.6-m² trawl.

males, 41% mature females, 2% immature males, and 12% immature females (Figure 1). The NMFS series captured 817 *A. trigonura*, of which 739 were examined; of these, 69% were mature males, 8% mature females, 1% immature males, and 22% immature females. The UH series with the IK captured 217 *A. trigonura* outside the Penguin Bank region (see below); of these, 54% were mature males, 24% mature females, 4% immature males, and 18% immature females. The UH neuston trawl series caught 25 *A. trigonura*; of these, 24 (96%) were mature females and one was a mature male.

The data from all trawling series show that immature squids are not being effectively sampled by any of these nets. Overall, only 4.4% of the catch from all trawl series consisted of squids <25 mm mantle length (ML). One series of tows off Penguin Bank, however, caught unusually high numbers of young: 35% of the 42 *A. trigonura* taken were <25 mm ML. This series also captured large numbers of oceanic fishes (Reid, unpubl. data) and oceanic squids (see below). A subsequent series of tows at the same locality off

Penguin Bank captured only one *A. trigonura* and one *P. giardi* Fischer and seven oceanics. That locality has maximum bottom depths of around 300 m but lies next to a steep drop-off that reaches depths of >1000 m and is frequently swept by strong tidal currents.

Excluding catches over the Penguin Bank region, *A. trigonura* was most abundant in the UH series over bottoms of 450–650 m. Only a few captures of *A. trigonura* were made over average bottom depths of <350 m (Figure 2). In contrast, the most successful of the four NMFS tows (station 29; 563 *A. trigonura* captured) was taken over bottom depths of 110–283 m along a steep slope (leeward O'ahu). Catch rates in the UH study were very poor relative to those taken in the other series. The average catch of this species in the UH series was 1.1 squid per tow (range, 0–19) for tows within its area of maximum abundance. This compares with an average of 204 per tow (range, 49–563) in the NMFS series and an average of 227 per tow (range, 66–787) in the HM series (Reid et al. 1991) or, in the latter case, an average of 22% of the entire catch of squids, fishes, and shrimps.
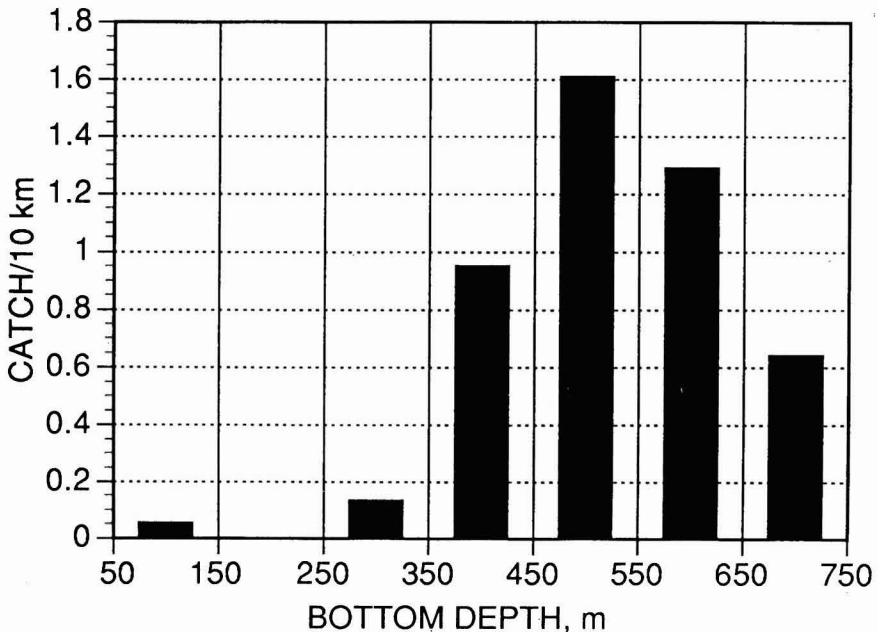
FIGURE 2. Catch rates of *Abralia trigonura* with the IK trawl over various bottom depths during the UH cruises. The rates are in units of 10 km because this is the approximate distance traversed by a single trawl and emphasizes the low capture rates.

Although similar comparative data are not available from the NMFS tows, inspection of the UH catches indicates that *A. trigonura* will be well less than 1% of the total catch. Clearly, the larger capacity of the HM and NMFS nets (4- to 5-fold more water filtered per tow) cannot explain the sampling discrepancies that exist.

At the peculiar Penguin Bank station, 11 IK tows caught 158 squids mostly belonging to four species: 42 *A. trigonura*, 15 *Pterygioteuthis giardi*, 77 *Abraliopsis pacificus* Tsuchiya & Okutani, and 19 *Abraliopsis* sp. A. The latter two species are members of the oceanic mesopelagic fauna. The four most successful catches of *A. trigonura* in the UH series, excluding Penguin Bank, were near dawn when the squid were apparently descending to their daytime depth.

In samples taken about 13 km offshore, *A. trigonura* ranked eleventh in abundance among all cephalopods (Young 1978). In contrast, 84% of the 984 cephalopods taken in the NMFS series were *A. trigonura* (59%

of the remaining cephalopods belonged to other boundary or facultative-boundary species). In the HM samples, *A. trigonura* composed 97% of all individuals among the 1644 cephalopods reported by Reid et al. (1991). In the UH samples taken with the IK, excluding those off Penguin Bank, which are more broadly spread over the boundary region than in the other trawling series, *A. trigonura* is also dominant but not as strongly. It was about four times more abundant than the second-ranked species, *Pterygioteuthis giardi*, and composed 51% of the 348 adult and subadult cephalopods captured. Boundary and facultative-boundary species composed 67% of all individuals among the 28 species of cephalopods captured.

SUBMERSIBLE OBSERVATIONS. *Abralia trigonura* was observed repeatedly from the submersible. Identification was based on size and shape, although on two occasions the diagnostic appearance of the ocular photophores was apparent. Nineteen sightings and

eight probable sightings were made. Most sightings (14 and 4 probable) occurred during a 15-min transect with the submersible cruising 10 m above the 435-m ocean bottom at 0.5 m/sec. A prior transect taken on a reciprocal course at the same locality with the submersible cruising 3–4 m above the bottom failed to detect any *A. trigonura*, nor did transects over bottoms of 535–540 and 270–275 m with the submersible cruising 2–3, 10, and 50 m above the bottom on separate transects at each site. Other observations were made during more general surveys. Three sightings and three probable sightings were made at midwater depths of 430–470 m, 10–100 m above the bottom. Single midwater sightings were also made at depths of 505 and 565 m, 85 and 25 m above the bottom. Only a single probable sighting was made where the squid was within 1 m of the bottom (550 m). The squid generally hung in the water with the fins moving. They occurred singly or occasionally in groups of two or three and were oriented either horizontally or obliquely with the head down. The sightings in the outer m-b zone correspond to the location of capture by most nighttime trawls.

Abralia astrosticta Berry

The UH series captured only advanced paralarval *A. astrosticta*, the largest of which was 14 mm ML. Of the 40 paralarvae captured, 90% were taken over bottom depths of <300 m, and all came from waters over bottoms of <400 m. The NMFS tows captured 56 *A. astrosticta* between 12 and 35 mm ML. The largest was an immature male. Eighty-four percent of these were taken on the leeward series that fished primarily in the inner m-b zone. The failure of the UH series to capture subadults in the inner m-b zone suggests that they do not usually enter the upper 200 m at night; although those caught by NMFS were within this zone, they could have been taken near the ocean floor. No *A. astrosticta* were taken by HM tows, all of which fished the outer m-b zone.

Compared with *A. trigonura*, *A. astrosticta* has distinctly larger photophores on its body.

Type C photophores (terminology from Young and Arnold [1982]) are 25% larger in diameter, and the lensed photophores (type A) are 100% larger. *Abralia astrosticta* also has a thicker mantle wall (25% thicker) compared with its congener of the same mantle length. Although the trawl data are meager, they suggest that *A. astrosticta* lives in the inner m-b zone during the day. The morphological data are consistent with this interpretation because squids in the inner m-b zone would benefit from larger photophores because of higher daytime light levels there than are typical for mesopelagic animals and from stronger swimming abilities because visual predators may be a greater threat in the more lighted waters.

Chiroteuthis imperator Chun

Reid et al. (1991) suggested this as a probable boundary species. Only a single chiroteuthid was taken in the UH or NMFS tows. It is a mature male *C. imperator* (155 mm ML) and was taken in a night horizontal tow that fished at a depth of ca. 300 m, suggesting that this species occurs below most of the depths trawled (<200 m) in these programs.

Enoploteuthis spp.

Species of this genus are members of the mesopelagic-boundary community in other localities (*E. chunii* Ishikawa, off Japan [Tsuchiya 1993]; *E. galaxias* Berry, off New Zealand [Riddell 1985]), but apparently none are members of the Hawaiian boundary community. We caught only a few specimens of this genus, but they represent all three Hawaiian species. The UH series caught two mature female *Enoploteuthis reticulata* Rancurel (75 and 99 mm ML); two *Enoploteuthis jonesi* Burgess (25 and 81 mm ML), one of which was a mature female; and one *Enoploteuthis higginsi* Burgess (39 mm ML). The HM series caught two *E. higginsi* (immature females, 38 and 15 mm ML) and one *E. jonesi* (mature female, 62 mm ML). All three species occur in oceanic areas well re-

moved from land (Burgess 1982, Tsuchiya 1993).

Haliphron atlanticus Steenstrup

Seven small specimens (10–45 mm ML) of this octopod were taken in seven separate tows on UH cruises. Five were caught at night in oblique tows to ca. 200 m depth near twilight, and two were caught in deep day tows 300 and 380 m over bottoms of ca. 400 m. Bottom depths for all captures ranged from 275 to 490 m. *Haliphron atlanticus* was not taken by the NMFS, the *Hokusei Maru*, nor by earlier extensive offshore sampling (Young 1978). However, 26 large individuals were taken by an earlier NMFS cruise (Burgess, unpubl. data, 1970) during the day in a bottom trawl that fished from 640 to 730 m, and single individuals were taken in two other bottom trawls at depths of 512 m (night) and 210 m (day).

Thore (1949) in his review of this species noted that most captures were made in proximity to land. He suggested that this octopus might not be entirely pelagic but may spend most of its life on the bottom on the continental shelves. He also offered the possibility that they may return to the bottom for egg-laying. In extensive plankton trawling around the Hawaiian Islands, only a single paralarva has been captured (pers. obs.).

SUBMERSIBLE OBSERVATIONS. A single large female estimated to be just over a meter in total length was observed barely moving over a bottom 270 m deep and not more than a few centimeters above it. The octopus was horizontal, with the arms extending anteriorly. As the submersible approached, the octopus began to swim more rapidly but still slowly, using a medusoid motion of the arms and web. When the arms spread out, a lightly colored egg cluster was seen attached near the mouth (Figure 3*A*). Individual eggs were considerably smaller than the suckers, and they were grouped into numerous grapelike clusters forming one large mass of eggs that swayed freely with the water movements. The movements of the octopus were weak, and the animal was badly damaged. The four

dorsal arms terminated in broad stubs that had not healed over (Figure 3*B*). Two of the four ventral arms were also incomplete, but not to the extent of the dorsal ones. A large wound marked by a sharp indentation on the dorsolateral surface of the head was emphasized by a patch of dark brown chromatophores (Figure 3*B*). Maneuvering the submersible to get a better photograph of the egg mass disturbed the bottom sediment, which formed a large cloud, and the octopus was lost.

Heteroteuthis hawaiiensis (Berry)

Nesis (1993) suggested that distributions of *Heteroteuthis* spp. are related to submarine rises and assumed that they spawn on the ocean floor. The UH series captured only six specimens; one was a subadult, but the remaining five were mature females. None was taken in the NMFS series.

Iridoteuthis iris (Berry)

Five individuals (9–11 mm ML) were taken in four UH night oblique tows whose maximum depths were 195–221 m. Bottom depths varied from 375 to 445 m. None was taken in any of the NMFS series.

Liocranchia reinhardti Steenstrup

Reid et al. (1991) considered *L. reinhardti* to be a possible boundary species. The UH series caught nine squid, mostly in standard tows, with a ML > 59 mm (60–118 mm ML). Three were taken over a bottom of 270 m, two at 460 m, and the rest at 500–675 m. In the NMFS series, one (140 mm ML) was taken in one leeward tow, and six (88–100 mm ML) were taken in one windward tow.

Nototodarus hawaiiensis (Berry)

Six female squid were taken in the UH tows; four were mature (113–141 mm ML). None was taken in the other series. A female (141 mm ML) had 1500 eggs in both oviducts. Mature eggs were amber yellow and measured 1.1 by 0.9 mm. Many sperma-
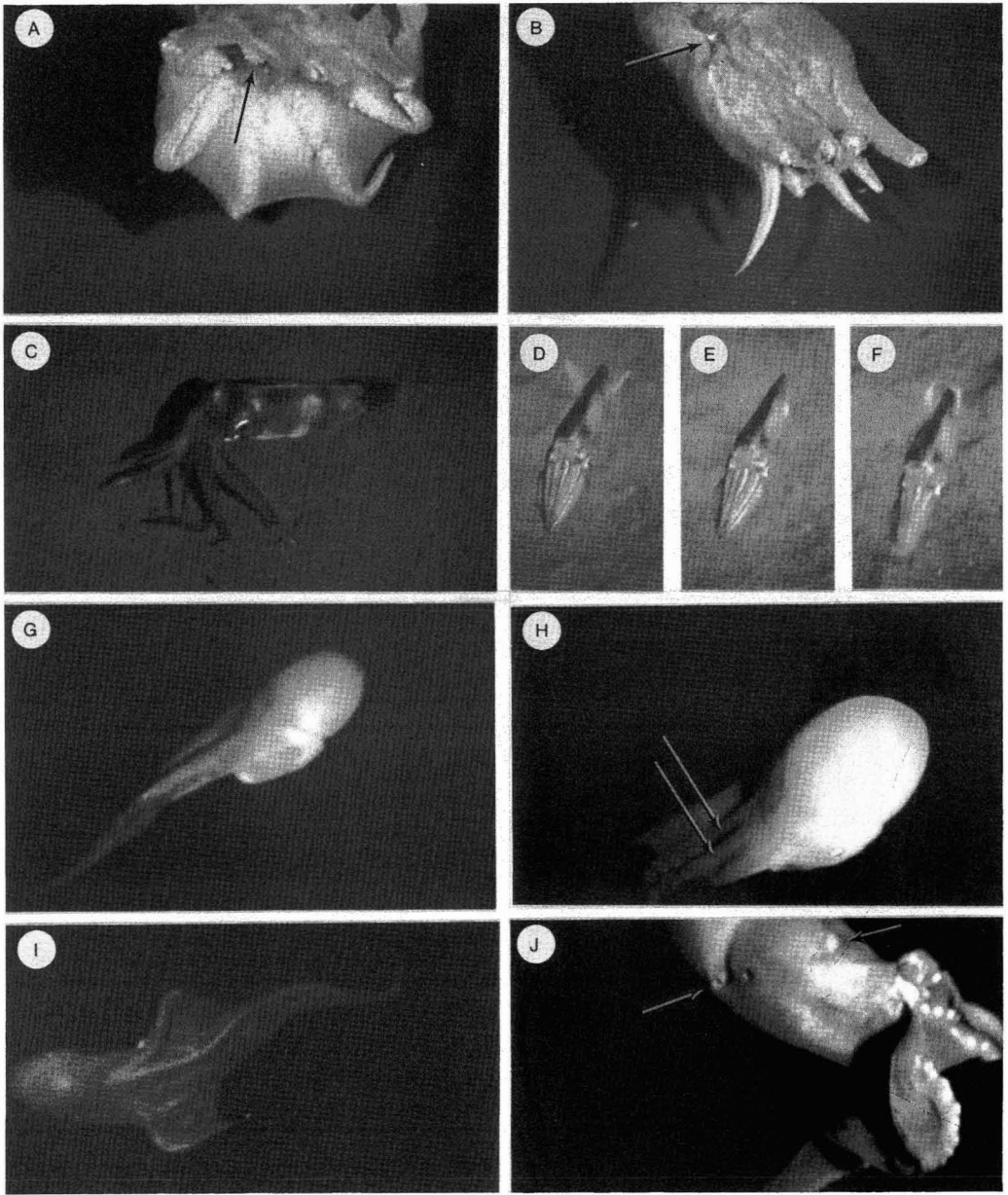
FIGURE 3. *A, Haliphron atlanticus,* partial oral view of arms and web showing the edge of the egg mass (arrow) held near the mouth. *B, Haliphron atlanticus,* arrow points to wound in dorsal surface. Note truncated dorsal arms and irregular lengths of ventral arms. *C, Nototodarus hawaiiensis,* squid sitting on ocean floor at 400 m. Note chromatophore bars. *D, Nototodarus hawaiiensis,* showing maximum dorsal extension of fins during slow swimming. *E, Nototodarus hawaiiensis,* sequence following *D* in which fins are at the maximum ventral extension (i.e., next to mantle). *F, Nototodarus hawaiiensis,* maximum dorsal extension of fins in preparation for a "power stroke" (the final downward beat of the fins), which occurred in conjunction with a strong jet from the mantle that sent the squid out of sight. *G, Tremoctopus* sp., dorsolateral view with dorsal arms extended and ventral arms folded in toward mouth. *H, Tremoctopus* sp., dorsal view, which fails to show the presence of water pores on the head at the base of arms I (arrows). *I, Tremoctopus* sp., dorsal view showing the relative lengths of arms and web. *J, Tremoctopus* sp., the octopus has somersaulted dorsally after nearly bumping the submersible; the ventral surface is at the top of the photo. The left arrow points to exhalent opening at the dorsal edge of the mantle opening; the right arrow points to funnel.

tangia were attached to the lips and a few to the buccal membrane. This squid had a nearly full stomach that contained fish remains with one type of otolith very similar to that of the common mesopelagic-boundary myctophid *Benthosema fibulatum* and a few crustacean remains.

SUBMERSIBLE OBSERVATIONS. Twelve of the 13 sightings recorded on videotape were made at depths of 345–400 m; the other was made at 500 m. In the 350- to 400-m range, the sand and silt bottom was nearly flat, with small depressions and mounds. The squid were always single and usually resting on the bottom or swimming 10–20 cm above the bottom. When sitting on the bottom, the squid rested anteriorly on their downward bent arms and tentacles and posteriorly on the end of the mantle. The squid typically displayed a series of dark bands across the body and head, presumably in response to disturbance by the submersible (Figure 3C). When disturbed by the submersible, the squid resisted swimming and sometimes had to be physically prodded before swimming away. They often moved rather slowly, vigorously flapping their relatively small fins (like a bird flapping its wings) against the mantle when swimming (Figure 3D, E). This method of fin swimming contrasts with the use of "undulating fins" common in many cephalopods with long fins where waves of sinusoidal shape pass along the fins (Kier 1989, Wells and O'Dor 1991). When sufficiently disturbed, the squid abandoned this method of swimming and, with a strong beat of the fins (Figure 3F) and a simultaneous jet from the mantle, darted out of sight.

Onychoteuthis sp. C

Although three species of *Onychoteuthis* occur in Hawaiian waters (Young and Harman 1987), UH tows with the IK caught a single postparalarval specimen (17 mm ML) of *Onychoteuthis* sp. C. Two larger specimens, 74 and 91 mm ML, were caught in neuston tows over bottom depths of 560 and 450 m. Earlier cruises caught three squid of this species in neuston tows over bottoms of

ca. 812, 470, and 485 m. None was caught in the NMFS tows. Reid et al. (1991) reported four unidentified specimens from HM tows. The meager data available suggest that this is a boundary species. Vecchione and Young (unpubl. data) found a variety of captures of this genus from Hawaiian waters. Sp. C was the only species taken, as a subadult, within the boundary zone, and it has not been taken outside this zone.

Pterygioteuthis giardi Fischer

This species was not considered a boundary squid by Reid et al. (1991); however, data from the present series suggest that it may be a facultative-boundary species. Two common species in this genus, *P. giardi* and *P. microlampas* Berry, occur in Hawaiian waters (Young 1978). Neither was common in the UH series. However, 55 *P. giardi* and 27 *P. microlampas*, larger than 10 mm ML, were captured where bottom depths were <800 m. In contrast, Young (1978) reported captures of >700 members of the genus in offshore waters, and *P. microlampas* was five times more abundant than *P. giardi*. In the two NMFS leeward tows that fished mostly in the inner boundary zone, 83% of catches of this genus were *P. giardi* (25 of 30 captures); the windward series, which cut across the entire m-b region and entered the oceanic zone, had 94% *P. microlampas* (30 of 32 captures). *Pterygioteuthis microlampas* is the overwhelmingly more abundant species of paralarvae taken in plankton tows around the Islands (pers. obs.).

Tremoctopus violaceus Chiaie

This cosmopolitan species is, presumably, a transient in the boundary region. Small individuals of *T. violaceus* were not uncommon in neuston tows, but only 10 (8–32 mm ML) were taken in IK tows.

SUBMERSIBLE OBSERVATIONS. A large *Tremoctopus* of undetermined species was observed from the submersible. This is the first time a member of this genus has been observed in situ. The large female, roughly 1 m in

total length, was seen swimming slowly ca. 5 m above the ocean floor at 340 m depth. The dorsal pigmentation was a golden brown, and rather mild iridescence from the lateral/ventral side gave a golden sheen. No translucency of the tissues was apparent, however. This appearance is very different from the dark blue dorsal surfaces and silvery to golden lower surfaces seen in *T. violaceus*. The octopus hit or nearly hit the submersible and was momentarily lost. When located again, it was cruising slowly with the ventral four arms tucked in toward the mouth (Figure 3*G*). *Tremoctopus violaceus* has large water pores on the head at the base of arms I. Although we had several good views of the dorsal surfaces of the head on the video, no water pores could be seen (Figure 3*H*). The upper four arms were extended and slightly spread. The left arm I was well over twice the length of arms II, but the right arm I was shorter than arms II and terminated bluntly, and the web extended slightly beyond the arm stump. The web margin formed a continuous curve between the tip of left arm I and the tip of right arm II (Figure 3*I*). The octopod's response to the disturbance created by the submersible was sluggish, although at one point the arms spread and then collapsed to provide some additional thrust to the mantle (jellyfish style). Nevertheless, the escape response was feeble. Near the submersible, presumably because of submersible turbulence or increased swimming activity, the skin over the mantle and head was thrown into large ripples, indicating the presence of loosely adherent skin. A circular orifice that momentarily appeared at the upper edge of the mantle opening indicated that water was expelled at this point (Figure 3*J*). Although we had several good views of the dorsal and ventrolateral surfaces of the head, no water pores could be seen. The octopus again passed slowly over the submersible and could not be relocated.

Other Species

A variety of other species, presumed to be oceanic species, was taken in the UH tows within the boundary zone (excluding paralarvae and animals taken at Penguin Bank): one *Ancistrocheirus leseuri* (Orbigny) (28 mm ML); 15 *Abraliopsis* sp. A (15–49 mm ML but with only three larger than 24 mm ML); eight *Abraliopsis pacificus* (19–26 mm ML); one mature female *Ctenopteryx sicula* (Verany) (48 mm ML); one *Histioteuthis hoylei* (Goodrich) (45 mm ML); one *Hyaloteuthis pelagica* (Bosc) (37 mm ML); one *Lepidoteuthis grimaldi* Joubin (67 mm ML); four *Leachia pacifica* (Issel) larger than 30 mm ML (37–45 mm ML); nine *Megalocranchia fisheri* (Berry) larger than 40 mm ML (42–50 mm ML); one *"Onykia" carriboea* Lesueur (18 mm ML); four *Octopoteuthis nielseni* Robson (26–32 mm ML); one *"Onykia"* sp. (20 mm ML); 22 *Pyroteuthis addolux* Young (15–44 mm ML); three *Sthenoteuthis oualaniensis* (Lesson) larger than 20 mm ML (23–30 mm ML); one squid tentatively identified as *Tetronychoteuthis dussumieri* Orbigny (25 mm ML); one *Vitreledonella richardi* Joubin (25 mm ML, tow fished at 355 m at night); seven *Euprymna scolopes* Berry taken in IK tows (4–10 mm ML), but many small ones taken in neuston tows; and four *Argonauta argo* Linnaeus larger than 12 mm ML.

The largest *Argonauta argo* was an immature female (61 mm ML) that was captured alive and placed in an aquarium, where it survived for several days. In captivity it defecated a large number of fecal strands. Diameter of the strands was mostly between 0.3 and 0.6 mm. The surfaces were smooth, and the strands maintained their integrity despite rough handling. Many of the strands were composed exclusively of small granular material. Under high magnification, these granules were membrane-bound vesicles, mostly 15–20 μm in diameter, and contained relatively uniform smaller granules whose size varied between vesicles. These appear to be "boules" from the digestive gland. Other strands, generally with a darker color, contained large numbers of exploded and unexploded nematocysts of various sizes, and some had shell fragments, chaetognath spines, and tiny lenses. Species of *Argonauta* are sometimes found in association with jel-

lyfish (e.g., Kramp 1956, David 1965). The evidence reported here suggests that this association is, at least, partially predatory. Heeger et al. (1992) reached a similar conclusion.

The two NMFS tows that fished entirely within the boundary zone captured, in addition to the four boundary species reported above (781 individuals), the following oceanic species: seven *Abraliopsis* sp. A (15–25 mm ML), three *Abraliopsis pacificus* (16–22 mm ML), one *Pyroteuthis addolux* (18 mm ML), two *Pterygioteuthis microlampas*, and one *Enoploteuthis reticulata* (35 mm ML).

DISCUSSION

The differences in the abundance of the various life-history stages of *Abralia trigonura* in the different sampling series partially can be explained by differences in sampling time and depth. The HM tows were taken during evening twilight as the animals were migrating to the surface and sampled mature males and females approximately equally, suggesting an evenly balanced sex ratio for mature animals. The neuston tows caught mature females almost exclusively, indicating a near-surface habitat for these squid at night. The stratified oblique NMFS tows caught large numbers of mature males but few mature females, presumably because ship disturbance at the surface resulted in net avoidance by females. The oblique UH tows also undersampled mature females, apparently for the same reason. The UH tows, however, greatly undersampled mature males as well. The poor catches of mature males in that series was caused by either avoidance of the smaller trawl, trawl escapement, or failure to sample the appropriate habitat. Simple trawl avoidance is unlikely because other equally or more active animals (e.g., boundary myctophids) were well sampled. I conclude (1) that the distribution of *A. trigonura* is unusual along the leeward steep slope of O'ahu, which explains the differences between NMFS and UH catches, and that something concerning the distribution of

mature males changes after twilight migration, which explains the differences between the UH catches and the HM catches; (2) that excessive net escapement occurs through the larger mesh of the IK net; or (3) that the catch reflects some combination of these two alternatives.

The HM and UH trawl data suggest that *A. trigonura* is an inhabitant of the outer m-b zone. In contrast, the large catches made by NMFS suggest that it belongs to the inner m-b zone. Perhaps this species exhibits landward migration at night, and the NMFS series captured squid during this horizontal migration. The UH samples, which were designed to look for this, could not detect it, but sampling effectiveness was questionable. As a result, the problem is unresolved.

All series undersampled immature males and females of *A. trigonura*. On the basis of the growth and mortality estimates of this species (Young and Mangold 1994), the population size of immature females between 15 and 25 mm ML should be 2.7 times that of females between 25 and 45 mm ML. Clearly, they should be apparent in our samples even if some size selection occurs in the trawls. With the exception of a few tows over Penguin Bank, this small size class was virtually absent from all boundary sampling. Young stages, apparently, do not live in the upper 200 m at night within the boundary region. A series of tows taken with smaller trawls (8 m^2) in offshore waters (Young 1978) captured 50 *A. trigonura*, and 70% were <25 mm ML. Their presence in offshore waters and in the upper 200 m there (Young 1978) suggests that the young stages (i.e., ca. 12–24 mm ML) occur primarily outside the boundary zone. Immature females between 25 and ca. 35 mm ML were also underrepresented. Apparently, the boundary zone is primarily the habitat of mature individuals of this species. The scarcity of young *A. trigonura* in the m-b region is surprising, because their small size would seem to make them especially vulnerable in more offshore waters to being swept away from the Islands by ocean circulation. S. B. Reid (unpubl. data) found that the small lantern-

fish *Benthosema fibulatum* occurred in the outer regions of the m-b region, seaward of the larger sizes of this fish. Submersible observations suggest that, unlike the boundary shrimp *Sergia lucens* (Omori and Ohta 1981) and its Hawaiian counterpart, *Sergia fulgens* (J. Hirota, pers. comm.), *A. trigonura* generally stays >5 m above the ocean floor during the day.

There are two species of *Tremoctopus* known, *T. violaceus* and *T. gelatus* Thomas, and both occur in Hawaiian waters (Thomas 1977). The first is thought to be epipelagic and the second mesopelagic to bathypelagic in vertical distribution. The specimen observed was peculiar in several ways. *T. violaceus* has a bluish purple dorsal coloration. Observations on a preserved specimen in the University of Hawai'i collections showed numerous contracted reddish brown chromatophores on the dorsal surface. If the blue iridescence were to be disabled in the living octopus when at depth, the resulting color could well be that observed. The dorsal color, however, combined with the looseness of the skin over the mantle, our inability to detect water pores, the depth of observations, and the sluggish behavior of the octopus, suggest that it could be *T. gelatus*. However, the ventral iridescence and the lack of obviously translucent tissues suggest that it could be *T. violaceus*. Both species of *Tremoctopus* generally have arms I truncated as adults and usually contain a deep cleft in the web between the two truncated arms (Naef 1923, Thomas 1977). Portmann (1952) described a specimen of 67 mm ML with separate extensive webs associated with each dorsal arm that contained transverse lines apparently where the arm and web can be autotomized (see also Kramer 1937). The shape of the dorsal web in the specimen reported here is not easily reconciled with our previous knowledge of this animal.

The brooding habits of *Haliphron atlanticus* were unknown previously. Apparently, this species broods its young in a manner typical of some pelagic octopods (Young 1972, 1978). The cause of the severe damage to the brooding octopus is unknown. Pre-sumably, this octopus did not survive past the brooding period (at best), which is typically the case in benthic octopods.

The mesopelagic boundary region is one of the most poorly investigated habitats in the ocean and one of the more difficult to study. Animals in this habitat must deal with a variety of bottom influences, both topographic and biological, as well as accentuated tidal advection and mesoscale eddies that can transport animals out of this habitat. These conditions, presumably, contribute to strong variability in horizontal distribution patterns with locality and time, a near-surface nighttime habitat for some and a near-bottom daytime habitat for many. These factors make sampling extremely difficult.

Knowledge of the cephalopods of this region has been hampered by sampling difficulties and the virtual absence of near-bottom trawling. Species that are not vertical migrators have been poorly sampled, as is apparently the case with *Iridoteuthis iris* and *Chiroteuthis imperator*, or, perhaps, even missed completely. As a result, conclusions presented here on species composition and distribution are tentative. Currently, only a single mesopelagic cephalopod, *Abralia astrosticta*, is a candidate as a member of the inner m-b zone. *Abralia trigonura* is a member of the outer m-b zone, but may migrate at night into the inner zone at least at some localities. *Pterygioteuthis giardi* occurs throughout much of the world's tropical and subtropical oceans. Its abundance in the m-b region, relative to its congener, suggests that it is a facultative-boundary species. The evidence for *L. reinhardti* as a boundary species has been strengthened by the additional captures, and an active, presumably "epipelagic" squid, *Onychoteuthis* sp. C, appears to be a member of the m-b region.

In spite of the difficulty in sampling the mesopelagic-boundary fauna, the fauna offers great potential for future investigators because of the relatively easy access to the region and the intriguing problems presented by a mesopelagic fauna adapted to a slope habitat.

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