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Atlantid Heteropods as Living Substrata for Eggs of *Halobates sericeus* (Heteroptera: Gerridae)[1]

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ABSTRACT: Atlantid heteropods are collected occasionally in Hawaiian waters with yellow, narrowly elliptical objects attached to their shells. Examination of 139 of these objects from 72 atlantids showed that they consisted of an outer, clear capsule whose contents were usually yellow, although 16 were empty and four contained brown insects at an advanced stage of development. The latter were identified as preemergent nymphs of the Pacific pelagic seaskater or ocean strider, *Halobates sericeus* Eschscholtz. The maximal number of attached capsules was four, although most shells (79%) had one or two. Capsules averaged 0.93 mm long and 0.36 mm wide and were deposited on either the right, left, or both sides of the shell. All 72 atlantids with egg capsules were adult males. Exclusive usage of males by *H. sericeus* is suggested to result from swarming behavior by male atlantids at the water surface. Although egg capsules were recorded from eight species of atlantids, most (86%) were on *Atlanta turriculata* d'Orbigny and *A. fusca* Souleyet, two of the most strongly pigmented species. Hypothetically, these two species would be the most visually conspicuous to *H. sericeus* at the ocean surface.

THE HETEROPODA IS a superfamily of gastropod molluscs that includes three families: the Atlantidae, Carinariidae, and Pterotracheidae (Lalli and Gilmer 1989). All heteropods are holopelagic and show a number of reproductive adaptations to an oceanic life style. Males produce spermatophores, which are thought to be transferred by the sperm groove of the penis to the female during copulation (reviewed by Lalli and Gilmer [1989]). Copulation has been observed only in *Pterotrachea hippocampus* Phillipi (Harbison, pers. comm., cited in Lalli and Gilmer [1989]), although transfer of spermatophores was not seen. Fertilized eggs are released by the female in a continuous mucoid string that periodically detaches, except in *Firoloida desmaresti* Lesueur, where a permanent egg filament is present at the posterior end of the body (reviewed by Lalli and Gilmer [1989]).

Tesch (1949:51) was the first person to speculate on the physical appearance and the site of spermatophore deposition on female heteropods: "In my material of Atlantidae I found some females provided with a sausage-like object, glued to the shell, either on the right or left side, and once even on both sides. It occurred in *Oxygyrus keraudreni*, *Atlanta inclinata* and *A. turriculata*. I think that this remarkable sausage is a kind of spermatophor [sic]." He illustrated two of these objects, the first of which was 0.8 mm long and was attached to the right side of a small *O. keraudreni* (Lesueur) (1.9 mm diameter, exclusive of the keel [redrawn here in Figure 1*a*]), and the second was 0.7 mm long and was attached to the left side of a 2.7-mm *A. inclinata* Souleyet. The objects consisted of an outer, clear capsule with dark contents having no particular structure. Tokioka (1955) subsequently described a 1.5-mm specimen of *O. keraudreni* (sex of animal not indicated) from Japanese waters that had two "spermatophores" (0.64 and 0.71 mm long) at-

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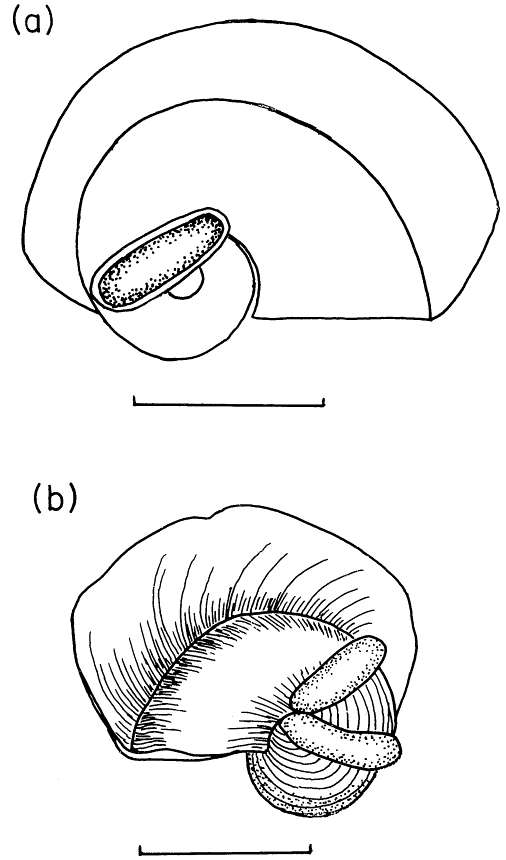

FIGURE 1. Sketches of *Oxygyrus keraudreni* with (*a*) a single *Halobates sericeus* egg attached to the right side of the shell, and (*b*) two *H. sericeus* eggs attached to the left side of the shell (from Tesch [1949] and Tokioka [1955], respectively). Scale bars = 1.0 mm.

tached to the left side of the shell (redrawn here in Figure 1*b*). Van der Spoel (1972 : 552) noted that all male atlantids he examined had "one and sometimes two spermatophores in development in the accessory sexual glands" adjacent to the penis, and that "the spermatophores found attached to the shell as described by Tesch (1949) are identical to those found in the sexual organs."

Detailed histological studies of the female reproductive system in atlantids by Thiriot-Quiévreux and Martoja (1974) showed that males deposit spermatophores directly in the female's mantle cavity. After deposition, the spermatophore sac ruptures and the spermatozoa escape and then swim to the genital tract. The findings of Thiriot-Quiévreux and Martoja raise the question: if the objects attached to the shells are not spermatophores, then what are they?

Since the early 1980s I have collected heteropods during cruises aboard research vessels in Hawaiian waters. The most abundant heteropods in the epipelagic zone off Hawai'i are the atlantids (Seapy 1990*a*). While sorting through the live plankton samples I occasionally came across atlantids with narrowly elliptical, clear capsules attached to their shells. The capsules were striking because their contents were bright yellow. During a cruise in 1991 when an extensive series of shallow plankton tows was taken, I sorted out a large number of atlantids that had these attached capsules. Their correct identity was finally solved when I encountered an atlantid with a capsule containing a brown insect that appeared to be a nymphal stage of a sea skater, *Halobates* sp.

MATERIALS AND METHODS

Specimens of atlantid heteropods with attached egg capsules were collected from Hawaiian waters during a number of cruises (Table 1). Plankton samples were taken in the epipelagic zone by oblique tows using open ring nets (1-m^2 and 4-m^2 mouth areas) and paired Bongo nets (0.38-m^2 mouth area each), and by surface neuston tows using manta nets. Atlantids were sorted from fresh plankton samples aboard ship, preserved in buffered 5% sea water–formalin solution, and transferred subsequently to 70% ethanol. Most egg capsules (92 on 45 atlantids) were collected during a cruise in February 1991. Five replicate oblique tows to a depth of about 100 m were taken with a 4-m^2 ring net at each of six locations, separated by ca. 1° latitudinal increments and extending northward to 27° N from the island of Kaua'i (at 22° 25′ N).

Shell diameters of specimens belonging to the three species of atlantids having the greatest numbers of attached egg cases were compared using two-sample Student's *t*-tests

TABLE 1

COLLECTION DATA FOR ATLANTID HETEROPODS WITH ATTACHED *H. sericeus* EGG CAPSULES FROM OCEANIC WATERS OFF HAWAI'I

DATE	LOCATION	NET TYPE	DEPTH (m)	NO. ATLANTIDS	NO. CAPSULES
4 Apr. 1984	Leeward O'ahu	Bongo	0–40	1	1
12 Apr. 1984	Leeward O'ahu	1 m^2	0–150	1	1
4 Aug. 1984	Leeward O'ahu	Bongo	0–140	1	2
22 Aug. 1985	Leeward O'ahu	1 m^2	0–150	1	2
10 Sept. 1985	Leeward O'ahu	Manta	surface	1	1
24 Mar. 1986	Leeward O'ahu	4 m^2	0–300	1	2
7 Aug. 1986	Leeward O'ahu	4 m^2	0–230	1	2
1/3 Nov. 1989	Leeward O'ahu	1 m^2	0–150	7	13
6–10 Feb. 1991	North of Kaua'i	4 m^2	0–100	45	92
10–16 Jan. 1992	Off Moloka'i, Lāna'i, Maui	1 m^2	0–75	13	22
Total				72	139

with the shell diameters of series of individuals of each species from representative plankton samples collected off leeward O'ahu in April 1984. Differences were considered significant if $P < 0.05$.

RESULTS

Seven egg capsules, at various stages of development, attached to four specimens of *Atlanta turriculata* d'Orbigny, were examined by L. Cheng, along with three male and three female *Halobates* collected off O'ahu with a manta net. She confirmed that the brown, late developmental stages were preemergent nymphs and identified the nymphs and adults as *Halobates sericeus* Eschscholtz, the Pacific pelagic seaskater or ocean strider. Because *H. sericeus* is the only species of *Halobates* recorded from oceanic waters in the vicinity and to the north of the Hawaiian Islands (Cheng 1989), all egg capsules on atlantid shells collected in this study are assumed to have been deposited by this species of *Halobates*.

Egg capsule contents were subjectively categorized at early, intermediate, or late stages of development. The early stage (Plate I*b*, upper right capsule) is bright yellow and contains no distinguishable internal structure. At the intermediate stage (Plate I*a*), parallel lines are evident along the ventral surface of the developing embryo. The ventral side of the egg is always oriented toward the viewer because the egg is cemented to the substratum on its dorsal side (Herring 1961; cited in Andersen and Polhemus [1976]). The parallel lines on the ventral surface of the embryo demarcate the developing rostrum, antennae, and front legs of the nymph. Also, the faint red rudiments of the paired compound eyes become evident at this stage. In the late stage, the yellow color of the embryo fades, and the developing nymph becomes brown. As the appendages become more defined, the brown color darkens and the eyes become bright red (Plate I*b*, middle capsule). After the nymph emerges, the clear capsule can remain attached to the atlantid shell (Plate I*b*, lower left capsule).

All 139 *H. sericeus* egg capsules were attached to the shells of adult male atlantids. When these atlantids were sorted from fresh plankton samples aboard ship, they always appeared to be healthy and not weakened by the presence of the capsules. Aside from the atlantids the only other living animals observed with attached *H. sericeus* capsules were two small *Janthina* sp. (2.40 and 2.42 mm shell width) collected in neuston tows; the first had one empty capsule on its shell, and the second had two empty capsules.

Halobates sericeus capsules were recorded from eight species of atlantids (Table 2), although most (70.8%) were on *Atlanta turri-*

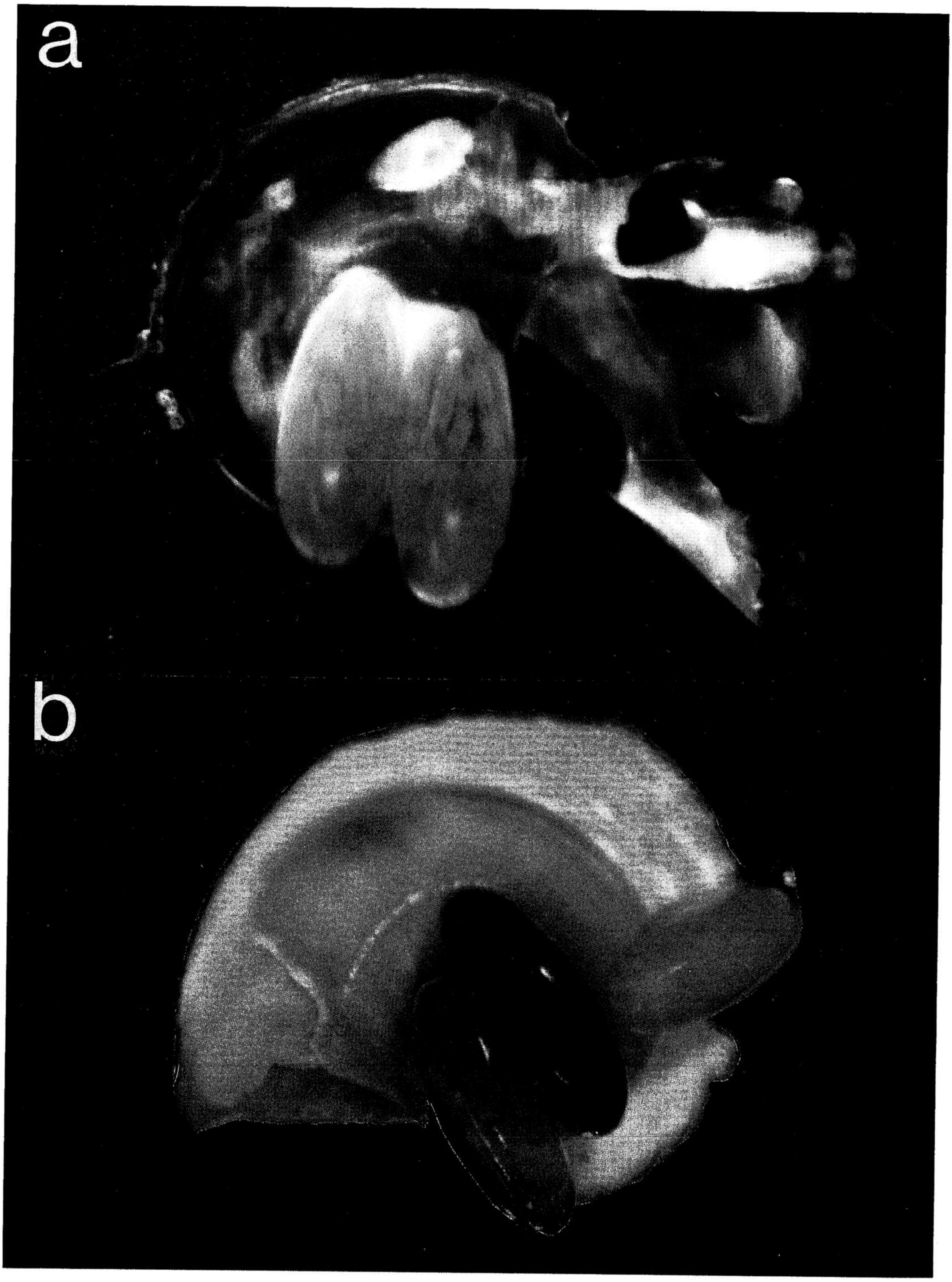

PLATE I. Photographs of (*a*) live *Atlanta turriculata* with pair of *Halobates sericeus* embryos at intermediate stage of development attached to right side of shell, and (*b*) preserved *A. turriculata* with three *H. sericeus* egg capsules at early, late, and posthatching (empty) stages.

TABLE 2

TOTAL NUMBERS AND CORRESPONDING PERCENTAGES OF ATLANTIDS WITH ATTACHED *H. sericeus* EGG CAPSULES (DATA BASED ON SPECIMENS FROM PLANKTON AND NEUSTON TOWS SUMMARIZED IN TABLE 1)

SPECIES	TOTAL	%
Atlanta turriculata	51	70.8
Atlanta fusca	11	15.3
Atlanta plana	4	5.5
Atlanta echinogyra Richter	2	2.8
Atlanta inflata	1	1.4
Atlanta lesueuri	1	1.4
Atlanta peroni Lesueur	1	1.4
Oxygyrus keraudreni	1	1.4

culata, with lesser numbers on *A. fusca* Souleyet (15.3%) and *A. plana* Richter (5.5%). Of the 139 capsules examined, 123 (88.5%) contained developing eggs and 16 (11.5%) were empty. Among those with developing eggs, 96 (78.1%) were at an early stage of development, 23 (18.7%) at an intermediate stage, and four (2.9%) at a late stage. The capsules averaged 0.93 mm in length and 0.36 mm in width ($n = 139$). The ranges in length and width measurements (0.88–1.00 mm and 0.32–0.42 mm, respectively) were narrow, and the resultant standard errors (0.01 mm) were very low.

Atlantid shells with attached *H. sericeus* egg capsules ranged in diameter (Figure 2) from 1.30 mm (a specimen of *Atlanta turriculata*) to 3.76 mm (a specimen of *A. plana*). For *A. turriculata*, *A. fusca*, and *A. plana*, the shell diameters of individuals with attached capsules exceeded 1.3, 1.4, and 2.3 mm, respectively. Atlantids are presumably grasped by *H. sericeus* for egg attachment when they are present at the sea surface. Under those circumstances, individual atlantids would be available to *H. sericeus* either because they periodically swim to the surface or because they are there as members of the neuston. To examine the first alternative, the size distributions of the three species of atlantids that were used most frequently by *H. sericeus* were compared with the sizes of individuals obtained from a representative series of plankton tows (Figure 2). In all cases, the atlantids used by *H. sericeus* were significantly larger than those available in the plankton (t-tests, $P < 0.01$). To examine the second alternative, atlantids were obtained from a series of neuston tows (Figure 3). Adult males were rarely captured, and nearly all postmetamorphic individuals were small (less than about 1.2 mm). There was no overlap in the size distributions of *A. turriculata* from the neuston and among those *A. turriculata* used by *H. sericeus* (Figure 2). Also, the species used most frequently by *H. sericeus*, *A. turriculata* (Table 2), ranked fourth in abundance in the neuston samples. The species that ranked second in usage by *H. sericeus*, *A. fusca*, was only represented by two specimens. Although the number of neuston tows examined was limited, these results suggest that adult atlantids are not usually present in the neuston.

The number of attached *H. sericeus* egg capsules ranged from one to four per shell (Table 3), although most shells (79.2%) had either one or two. Where a single capsule was present, the left and right sides of the shell were utilized equally. If two capsules were present, they were paired on one or the other side of the shell in 29 of 31 instances, and the right side of the shell was used somewhat more frequently than the left side (17 compared with 12 cases). In the 29 cases where the capsules were paired, their contents were at the same stage of development in all but three cases. Where three capsules were present, all three were on the same side in six of nine cases. Last, when there were four capsules per shell all were on the same side in only one of six instances, whereas capsules were deposited in pairs on each side of the shell in three cases. These results suggest that the small size of the shell limits the amount of area available for attachment, and that *H. sericeus* uses the largest area of unoccupied shell surface when space becomes limited.

The relationship between shell size and number of attached *H. sericeus* egg capsules was examined using the 42 specimens of *Atlanta turriculata* (Table 4). As the number of capsules increased from one to four, the minimal shell diameter increased from 1.30 to 1.58 mm. However, a similar relationship

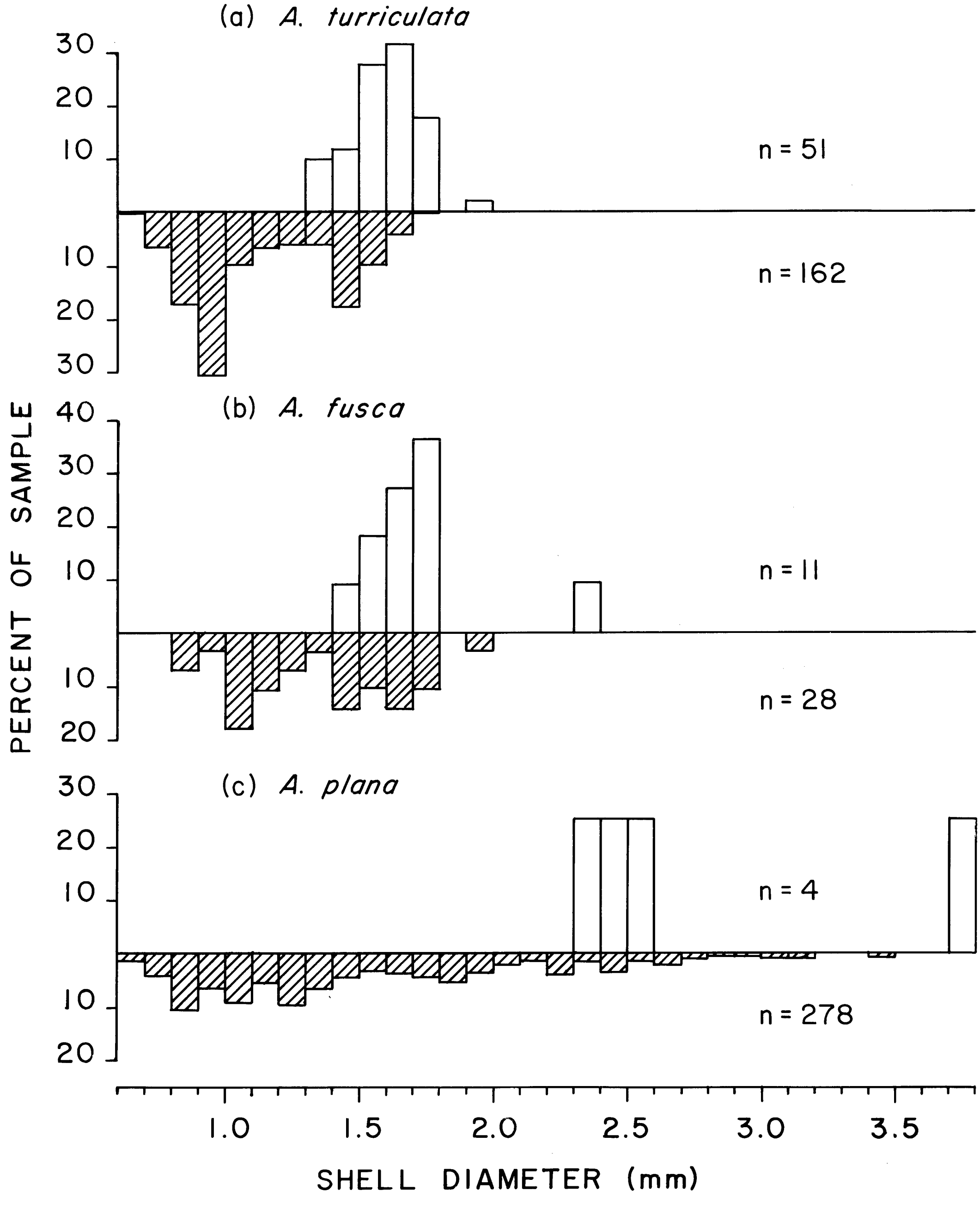

FIGURE 2. Size-frequency distribution of shell diameters for atlantid species with and without attached *Halobates sericeus* eggs. Shell diameter values were pooled into 1-mm size classes for (*a*) *Atlanta turriculata*, (*b*) *A. fusca*, and (*c*) *A. plana*. Open histogram bars are based on data from shells with attached *H. sericeus* eggs from this study. Shaded bars are based on data from a large series of Bongo net samples collected off leeward O'ahu in April 1984 (Seapy 1990*a*). Only postmetamorphic individuals (greater than about 0.6 mm) were included. Sample size (*n*) is indicated for each plot.

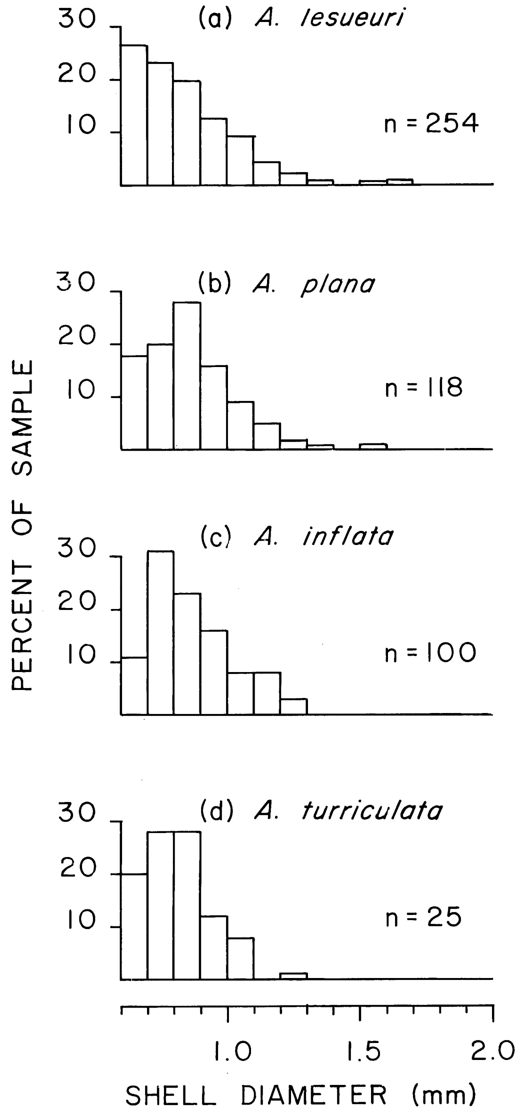

FIGURE 3. Size-frequency distribution of shell diameters arranged into 1-mm size classes for postmetamorphic individuals (greater than about 0.6 mm) belonging to (*a*) *Atlanta lesueuri*, (*b*) *A. plana*, (*c*) *A. inflata*, and (*d*) *A. turriculata*. Specimens were from 20 neuston tows taken off leeward O'ahu during 1985–1986. Sample size (*n*) is indicated for each plot.

was not seen for either the maximal or mean shell diameters, although the mean diameter for shells with a single attached egg (1.50 mm) was 0.11–0.13 mm less than that for shells with two, three, or four eggs.

TABLE 3

NUMBER AND LOCATION OF *H. sericeus* EGG CAPSULES ON RIGHT AND/OR LEFT SIDES OF ATLANTID SHELLS (EGG CAPSULE DATA POOLED FOR ALL SPECIES OF ATLANTIDS)

NO. EGG CAPSULES PER SHELL	SIDE OF SHELL				
	RIGHT	LEFT	BOTH	TOTAL	%
1	13	13	—	26	36.1
2	17[a]	12[b]	2	31	43.1
3	2	4	3	9	12.5
4		1	5	6	8.3

[a] In all but two cases the pairs of egg capsules were adjacent and at the same stage of development.

[b] In all but one case the pairs of egg capsules were adjacent and at the same stage of development.

TABLE 4

SHELL DIAMETERS OF *Atlanta turriculata* IN RELATION TO THE NUMBER OF ATTACHED *H. sericeus* EGG CAPSULES

PARAMETER	NO. EGG CAPSULES			
	1	2	3	4
Mean diameter (mm)	1.50	1.61	1.62	1.63
Minimal diameter (mm)	1.30	1.35	1.44	1.58
Maximal diameter (mm)	1.62	1.90	1.70	1.68
Sample size	12	20	6	4

DISCUSSION

Halobates spp. have been reported (Andersen and Polhemus 1976, Cheng 1985) to deposit their eggs on a variety of objects floating on the ocean surface: seeds, seaweed, cork, timber, tar lumps, coal, *Spirula* and *Sepia* shells, insect carcasses, and seabird feathers. For live animals, the only record of egg attachment is on the tail feathers of the common noddy, *Anous stolidus* (L.) (Andersen and Polhemus 1976). The report presented here of *H. sericeus* egg capsules on the shells of live atlantids represents the first record of *Halobates* eggs deposited on living marine invertebrates or on substrates as small as an atlantid shell (L. Cheng, pers. comm.).

Cheng (1973) reported that *Halobates* spp. can lay up to 25–30 eggs at a time, and Andersen and Polhemus (1976) illustrated nine

Halobates sp. eggs laid side by side. In the study presented here pairs of eggs at the same apparent stage of development were adjacent to each other in many instances. Individual females were probably responsible for depositing such egg pairs.

A perplexing problem is why all atlantids with attached egg capsules were adult males. Based on the series of neuston tows examined in this study (Figure 3), adult males usually do not seem to be present in the neuston. Under what circumstances, then, do males occur at the surface? One possibility is suggested by the finding of Seapy and Richter (1993) that high densities of adult males belonging to three species (*Atlanta californiensis* Seapy & Richter off southern California and *A. oligogyra* Tesch and *Protatlanta souleyeti* [Smith] from the central Atlantic Ocean) occasionally are collected in the neuston during the daytime. They speculated that males may swarm at the ocean surface for mating, possibly in the same manner that male mosquitoes (and other dipterans) form large aerial mating aggregates (reviewed by Downes [1969]). In those insects a female enters a swarm briefly, is captured by a male, and then drops out of the swarm to mate. Downes considered this mating behavior to serve as a mechanism of bringing together males and females in low-density populations where the individuals are usually dispersed. Most atlantid populations off Hawai'i also occur in low densities and are dispersed vertically in the water column (Seapy 1990*a*) (e.g., the population densities of *A. turriculata* and *A. fusca* average about five and one individuals per 1000 m^3, respectively, and range from the surface to about 100 and 200 m, respectively).

TABLE 5

NUMBERS AND PERCENTAGE OF SPECIMENS BELONGING TO THE 13 SPECIES OF ATLANTIDS COLLECTED BY PLANKTON NET TOWS IN HAWAIIAN WATERS BETWEEN 1984 AND 1986 (FROM SEAPY 1990*b*)

SPECIES	TOTAL NO. COLLECTED	%
Atlanta lesueuri	2,031	27.0
Atlanta turriculata	1,085	14.4
Atlanta plana	1,059	14.1
Atlanta inflata	1,052	14.0
Atlanta peroni	863	11.5
Protatlanta souleyeti	589	7.8
Atlanta meteori Richter	338	4.5
Atlanta oligogyra	194	2.6
Atlanta helicinoides Souleyet	173	2.3
Atlanta fusca	57	0.8
Atlanta echinogyra	47	0.6
Atlanta tokiokai van der Spoel & Troost	25	0.3
Oxygyrus keraudreni	14	0.2

Most *H. sericeus* egg capsules were attached to *A. turriculata* and *A. fusca*. If *H. sericeus* exhibited no selectivity among the species of atlantids available as substrata for egg deposition, then these two species should be the most abundant atlantids in the Hawaiian plankton. However, this does not appear to be the case (Table 5); *A. turriculata* ranked second (14.4%) to *A. lesueuri* Souleyet (27.2%) and was close in abundance to *A. plana* (14.1%) and *A. inflata* Souleyet (14.0%), but *A. fusca* was uncommon, ranking tenth (0.8%) among the 13 species. A possible explanation of the preferential selection of *A. turriculata* and *A. fusca* is that both of these species possess dark body pigmentation (Seapy 1990*b*), which could increase their visibility to *H. sericeus*. *Atlanta fusca* is amber to brown, and *A. turriculata* is reddish brown (strongest in the spire region). Except for *Oxygyrus keraudreni*, which is translucent bluish purple, all other Hawaiian atlantids are clear or have pigmentation that is largely restricted to the shell sutures. *Halobates* spp. are considered to have well-developed eyes that are used for prey location and predator avoidance (Cheng 1985). One would assume, then, that they locate atlantids visually and that the most darkly pigmented species would be easiest to find. Because female *A. turriculata* and *A. fusca* display the same pigmentation as males, there is no reason to expect that *H. sericeus* could distinguish between the two sexes and only select males. This problem is resolved, however, if the only atlantids large enough to serve as substrata for egg deposition are adult males that swarm periodically at the sea surface.

Halobates sericeus eggs can take up to a month to hatch (Cheng 1985). Thus, eggs de-

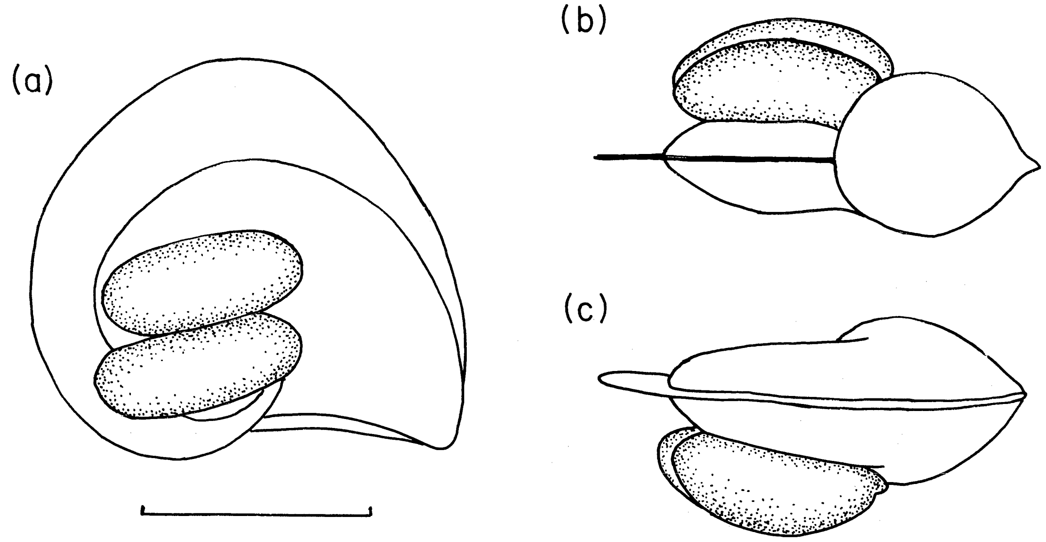

FIGURE 4. Sketches of a 1.7-mm *Atlanta turriculata* with two *Halobates sericeus* eggs attached to the right side of the shell. Views of (*a*) right side, (*b*) ventrum, and (*c*) dorsum. Scale bar for all sketches = 1.0 mm.

posited on atlantid shells may create buoyancy and drag problems over an extended period of time. If the eggs are positively or negatively buoyant, the atlantid would have to expend additional swimming energy to maintain its position in the water column. Also, because the egg capsules are large relative to the size of the atlantids, they would create drag during swimming (Figure 4). Perhaps the high percentage of capsules containing early (78%) and intermediate (19%) developmental stages are indicative of a high mortality cost to the atlantids. Also, one wonders about the fate of nymphs that presumably hatch while the atlantids are submerged.

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