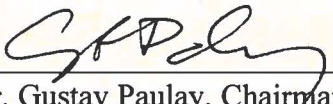AN ABSTRACT OF THE THESIS OF Linda A. Ward for the Master of Science in Biology presented May 22, 1998.

Title: *Octopus brachiotomus*, sp. nov. (Cephalopoda: Octopodidae), a new shallow-water, arm-autotomizing octopus from Guam; and arm autotomy in *Octopus brachiotomus* from Guam

Approved: _____
Dr. Gustav Paulay, Chairman, Thesis Committee

A new littoral, arm-autotomizing octopus from Guam is described. *Octopus brachiotomus* sp. nov. is a small intertidal species, known as yet from reef flats only around Guam. This species is capable of shedding arms, autotomized distal to suckers 4-7 on the arm base. Its long arms, arm autotomy, complex skin sculpture and color patterns, long hectocotylized arm with small narrow ligula, arm and web formulas, and enlarged suckers on arm pairs II and III of mature males, place this new species within the *Octopus horridus* group. Notes on habitat preferences, activity patterns, estimated lifespan of approximately seven months, egg production, hatchling characteristics, female brooding behavior, and senescence are also given.

Octopus brachiotomus, a small, shallow-water octopus from Guam exhibits arm autotomy. Loss of the hectocotylized right third arm of males used for sperm transfer could significantly reduce fitness of the semelparous male, depending on arm regeneration time. Enlarged suckers on the males of some species have been suggested to play roles in mate attraction or detection and to provide heightened chemosensitivity of receptive females. Tests of autotomy showed that the hectocotylized male arm is

preserved from autotomy, but arms bearing enlarged suckers are not preserved from autotomy. Regeneration from autotomy was found in approximately 20% of animals in the field, while regeneration from other causes occurred in over twice as many individuals. Arms completely regenerated from autotomy in approximately 10 weeks, as measured on captive animals. Incidence of arm autophagy was noted in animals held through to senescence. No plane of weakness or mechanism of autotomy was found by histological examination, using light microscopy, of the arm autotomy zone.

TO THE OFFICE OF GRADUATE SCHOOL AND RESEARCH

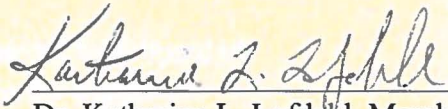The members of the committee approve the thesis of Linda A. Ward, presented May 22, 1998.
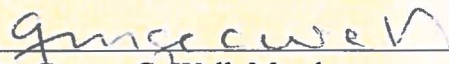
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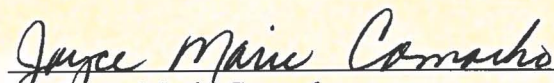
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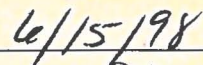
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6/15/98
Date

OCTOPUS BRACHIOTOMUS, SP. NOV. (CEPHALOPODA: OCTOPODIDAE),
A NEW SHALLOW-WATER, ARM-AUTOTOMIZING OCTOPUS FROM
GUAM; ARM AUTOTOMY IN *OCTOPUS BRACHIOTOMUS* FROM GUAM

BY

LINDA ALICE WARD

A thesis submitted in partial fulfillment of
the requirements for the degree of

MASTER OF SCIENCE

IN

BIOLOGY

UNIVERSITY OF GUAM

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Acknowledgments

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Chapter 2: Arm autotomy in *Octopus brachiotomus* from Guam

Chapter 1

Octopus brachiotomus, sp. nov. (Cephalopoda: Octopodidae), a new shallow-water, arm-autotomizing octopus from Guam

A new littoral, arm-autotomizing octopus from Guam is described. *Octopus brachiotomus* sp. nov. is a small intertidal species, known as yet from reef flats only around Guam. This species is capable of shedding arms, autotomized distal to suckers 4-7 on the arm base. Its long arms, arm autotomy, complex skin sculpture and color patterns, long hectocotylized arm with small narrow ligula, arm and web formulas, and enlarged suckers on arm pairs II and III of mature males, places this new species within the *Octopus horridus* group. Notes on habitat preferences, activity patterns, estimated lifespan of approximately seven months, egg production, hatchling characteristics, female brooding behavior, and senescence are also given.

Introduction

Little is known of the octopod fauna of Guam and the Mariana Islands. Recent exploration of Guam's intertidal fauna has led to the discovery of a small octopus (Fig. 1.1) on intertidal reef flats. This species has proven to be an undescribed member of the *Octopus horridus* species group of Norman (1993a) and Norman and Sweeney (1997).

The members of the *Octopus horridus* species group are small, shallow-water octopuses, all with elongate arms, well-developed cryptic color patterns and sculpture, moderately low gill lamellae count (5-6 per demibranch), and the capacity for arm autotomy and regeneration close to arm bases. Species of the group are primarily day-active, foraging on intertidal coral and rocky reefs.

Autotomy, the severance of an appendage at a preformed breakage plane and followed by regeneration, is known in several phyla and molluscan orders (Stasek 1967). Autotomy among octopods is apparently restricted to long-arm species (Norman 1993a), including all species of the *Octopus horridus* species group (Table 1.1).

Figure 1.1. *Octopus brachiotomus* in *Padina* sp. alga showing raised papillae on dorsal mantle.

Other incirrate octopods known to autotomize arms include *Tremoctopus*, *Ocythoe* and *Argonauta* (Stasek 1967), *O. defilippi* Vérany, 1851, *O. alecto* Berry, 1953, *Euaxoctopus panamensis* Voss, 1971, *E. pillsburyae* Voss, 1975, and *Ameloctopus litoralis* Norman, 1992 (Norman 1992, 1993a).

The *Octopus horridus* group, prior to the description presented here, was comprised of 13 described and 3 undescribed species. The group is endemic to the Indo-West Pacific, ranging from the Red Sea to Hawaii, north to Japan, and south to Natal, South Africa. Norman recently (1993a) identified seven members of this group in North Australia waters.

Table 1.1. Member species of the *Octopus horridus* group (Norman 1993a, Norman and Sweeney 1997).

Species	Type locality
Octopus abaculus Norman and Sweeney 1997	Philippines
Octopus aculeatus d'Orbigny, 1826	Philippines
Octopus arborescens (Hoyle, 1904)	Ceylon (Sri Lanka)
Octopus argus Krauss, 1848	Natal Prov., South Africa
Octopus bandensis Hoyle, 1885	Banda, Indonesia
Octopus filamentosis Blainville, 1826	Mauritius
Octopus quangdongensis Dong, 1976	Quangdong Prov., China
Octopus harmandi de Rochebrune, 1882	South Vietnam
Octopus horridus Audouin *in*: Audouin & Savigny, 1826	Red Sea
Octopus mutilans Taki, 1942	Japan
Octopus niveus Lesson, 1830	Bora Bora (Society Is.)
Octopus tenebricus Smith, 1884	GBR*, Australia
Octopus tonganus Hoyle, 1885	Tonga
Octopus sp. 1 Norman, 1993	[GBR, Australia]
Octopus sp. 2 Norman, 1993	[GBR, Australia]
Octopus sp. 2 Norman and Sweeney, 1997	[Philippines]
	*Great Barrier Reef

Omitted are *Octopus aranea* d'Orbigny, 1835, junior synonym of *O. filamentosis* and *Octopus fimbriatus* Ruppell *in*: Férussac & d'Orbigny, 1840, junior synonym of *O. horridus* (Norman pers. comm.)

Materials and Methods

Field collections were made mainly by intertidal reef walking during day and night low tides. A few animals were also collected in subtidal locations by snorkel and SCUBA. Of 123 individuals encountered live on Guam's leeward and windward reefs between January 1993 and May 1995, 78 were found during daylight low tides, 45 during night low tides. Of these, 32 females and 44 males were collected. Animals were maintained in captivity for a few hours to 151 days. Of those collected, 19 females and 30 males were anesthetized in gradually cooled seawater for at least three hours, rinsed in freshwater, fixed in 10% formalin for a minimum of two weeks, measured, then preserved in 80% ethanol (Roper and Sweeney 1983). Weights are of ethanol preserved specimens. In addition, 3 females and 5 males that died in captivity were similarly

preserved. A few specimens were measured both as freshly killed and as fixed specimens; comparisons of the measurements indicate minimal fixation shrinkage, though 5-10% shrinkage occurred after storage in ethanol.

The holotype, allotype, and paratypes have been deposited in the National Museum of Natural History, Washington (USNM). Paratypes have also been deposited in the University of Guam Invertebrate Systematic Collection (UGI), the Museum of Victoria, Australia (NMV), Bishop Museum, Honolulu (BMH), California Academy of Science, San Francisco (CASIZ), and Santa Barbara Museum of Natural History (SBMNH).

The description, tables, measurements (in mm), and indices follow Roper et al. (1983: 55-56) and Toll (1988), augmented by Norman's (1993a) added and modified indices, symbols and terminology (Figure 1.2, Appendix I). Hatchling measurements and description of chromatophore patterning follow Young et al. (1989) and Sweeney et al. (1992). Descriptions are based on submature and mature specimens. Juveniles undergo considerable ontogenetic change in early growth stages, which can confuse diagnostic characters (Norman and Sweeney 1997). Values for both the holotype and other specimens are given in parentheses: the first number refers to the holotype, followed by the range with underlined mean (cf. Norman 1993a), e.g. head width index (HWI 57.1; 34.1-52.6-72.7).

Material examined

Of 123 animals encountered live in intertidal and shallow subtidal reef flats of Guam, 76 were collected. The holotype, allotype, and several paratypes have been deposited in

the USNM collection. Counts and indices for the holotype and other male specimens are presented in Table 1.2, for the allotype and other female specimens in Table 1.3.

Holotype: 28 mm ML ♂ (USNM 885669) Reef flat in front of University of Guam Marine Lab, Pago Bay, Guam, 144° 47′ E, 13° 25′ N, < 0.1 m, L. A. Ward, 5 Apr 1995 (active at 16:33 hr).

Allotype: 26 mm ML ♀ (USNM 885670) Location and depth as holotype, L. A. Ward, 2 Apr 1995 (active at 15:29 hr).

Selected specimens studied: Pago Bay: Approx. 7 mm ML ♀ (UGI unreg.) Location and depth as holotype, L. A. Ward, 13 May 1995 (active at 13:20 hr), maintained in captivity 151 days through maturity and egg laying;

15 mm ML ♀ (UGI unreg.) Location and depth as holotype, L. A. Ward, 6 Mar 1994 (active at 20:40 hr);

18 mm ML ♀ (USNM unreg.) Location and depth as holotype, K. L. Lofdahl, 19 Nov 1994 (active at 01:51 hr);

20 mm ML ♀ (USNM unreg.) Location and depth as holotype, L. A. Ward, 19 Nov 1994 (active at 01:23 hr);

24 mm ML ♀ (USNM unreg.) Location and depth as holotype, C. Bassler, 21 Aug 1994 (active at 14:00 hr);

24 mm ML ♀ (NMV F80723) Location and depth as holotype, L. Ward, 22 Mar 1994 (active at 21:09 hr);

26 mm ML ♀ (UGI unreg.) Location and depth as holotype, S. Hughes, 24 Mar 1994 (active at 23:00 hr);

28 mm ML ♀ (BMH unreg.) Location and depth as holotype, K. L. Lofdahl, 19 Nov 1994 (active at 02:18 hr);

21 mm ML ♂ (NMV F80719) Location and depth as holotype, L. A. Ward, 24 Jan 1994 (active at 23:05 hr);

22 mm ML ♂ (UGI unreg.) Location and depth as holotype, L. A. Ward, 27 Aug 1993 (active at 10:40 hr);

23 mm ML ♂ (UGI unreg.) Location and depth as holotype, K. L. Lofdahl, 8 Jul 1994 (active at 11:40 hr);

24 mm ML ♂ (SBMNH unreg.) Location and depth as holotype, S. Hughes, 24 Mar 1994 (active at 23:00 hr);

25 mm ML ♂ (NMV F80720) Location and depth as holotype, A. Santana, 29 Apr 1994 (active at 14:40 hr);

27 mm ML ♂ (NMV unreg.) Location and depth as holotype, J. Chamberlain, 23 May 1994 (active at 14:00 hr).

Adelup: 30 mm ML ♀ (NMV F80721) Reef flat south of Governor's complex, Adelup, Guam, 144°43′ E, 13°28′ N, < 0.1 m, K. L. Lofdahl, 25 May 1994 (active at 12:40 hr);

33 mm ML ♀ (UGI unreg.) Location and depth as NMV F80721, L. A. Ward, 24 May 1994 (found at 12:35 hr with only 1 arm);

19 mm ML ♂ (USNM unreg.) Location and depth as NMV F80721, K. L. Lofdahl, 7 Aug 1994 (active at 12:22 hr);

24 mm ML ♂ (SBMNH unreg.) Location and depth as NMV F80721, K. L. Lofdahl, 7 Aug 1994 (active at 12:32 hr);

25 mm ML ♂ (NMV F80722) Location and depth as NMV F80721, K. L. Lofdahl, 25 May 1994 (active at 12:05 hr);

26 mm ML ♂ (UGI unreg.) Location and depth as NMV F80721, K. L. Lofdahl, 26 May 1994 (active at 12:03 hr);

28 mm ML ♂ (USNM unreg.) Location and depth as NMV F80721, K. L. Lofdahl, 12 Apr 1995 (active at 23:30 hr);

32 mm ML ♂ (BMH unreg.) Location and depth as NMV F80721, K. L. Lofdahl, 7 Jul 1994 (active at 12:00 hr);

33 mm ML ♂ (NMV unreg.) Location and depth as NMV F80721, K. L. Lofdahl, 10 Apr 1995 (active at 21:43 hr);

35 mm ML ♂ (USNM unreg.) Location and depth as NMV F80721, L. A. Ward, 30 July 1993 (active at 10:30 hr).

Etymology: This species derives its name from the Greek *brachios* meaning 'arm;' and the suffix *-tomy* denoting 'cutting, dissection.'

Diagnosis: Small, but larger than pygmy species, ML to at least 35 mm. Arms moderately long, commonly 4-5 times mantle length (Fig. 1.3a). Dorsal arms shortest, grading to ventral arms longest. Webs moderately shallow, about 15% of longest arm; dorso-lateral and ventro-lateral webs deepest, ventral and dorsal webs shallowest. Suckers moderate-size, 9-12% of ML, forming two off-set (biserial) rows. Sucker counts about 120 in males, 135 in females on normal dorsal arms, and about 145 in males
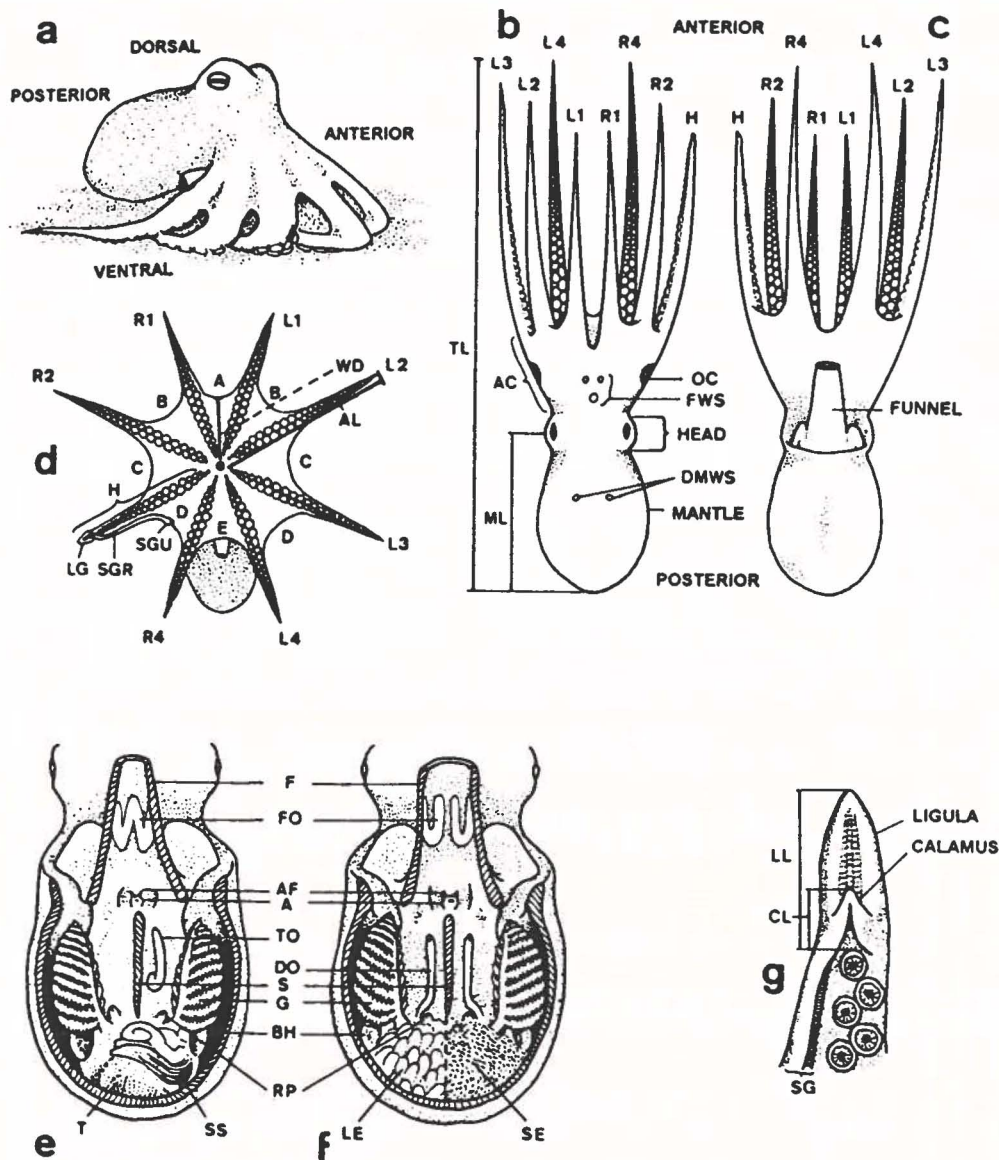
Figure 1.2. Orientation, terminology and measurements. **L** = left; **R** = right. *a*, Orientation relative to live animal. *b-c*, Whole animal; *b*, dorsal view; *c*, ventral view; **AC** = arm crown; **DMWS** = dorsal mantle white spots (*sensu* Packard and Sanders 1971); **H** = hectocotylized arm in males; **ML** = mantle length; **ST** = position of stylets; **TL** = total length. *c*, Whole animal, ventral view. *d*, Oral view of arms and webs in males: **AL** = arm length; **H** = hectocotylized arm; **LG** = ligula; **SGR** = spermatophore groove; **SGU** = spermatophore guide; **WD** = web depth. Webs designated from dorsal to ventral sectors by letters **A** to **E**. Arms numbered from dorsal to ventral as 1-4. *e-f*, Mantle cavity contents: **A** = anus; **AF** = anal flaps; **BH** = branchial hearts; **F** = funnel; **FO** = funnel organ (W shape shown on male, UU shape shown on female); **G** = gills; **S** = septum. *e*, Mantle cavity contents of mature male: SS, spermatophore storage sac; T, testes. *f*, Mantle cavity contents of mature female: **DO** = distal oviducts; **LE** = mature ovary as in "large-egg" species; **SE** = mature ovary as in "small egg" species. *g*, Components of hectocotylized arm tip of mature male: **CL** = calamus length; **LL** = ligula length; **SG** = spermatophore groove. (Modified from Norman and Sweeney 1997.)

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Table 1.2. Measurements (mm) and indices of male *Octopus brachiotomus*, sp. nov. al, autotomized arm lost; ar, arm regenerating; ap, arm autophagy; da, damaged; in, indistinct su, submature; ma, mature; se, senescing; —, not recorded.

				Museum Registration Number				
Abbreviations as in Appendix I	USNM unreg.	SBNMH unreg.	BMH unreg.	USNM unreg.	NMV unreg.	NMV unreg.	USNM 885669 Holotype	SBMNH unreg.
ML	22	24	26	26	27	27	28	30
StM	ma	su	ma	ma	su	se	ma	ma
TL	131	128	123	162	148	153	177	158
TWt, g	8.5	8.4	13.0	12.7	11.0	12.4	12.4	14.3
MWI	77.3	75.0	69.2	73.1	55.6	55.6	71.4	63.3
HWI	72.7	45.8	57.7	65.4	44.4	51.9	57.1	50.0
MAI	21.0	23.8	25.5	20.6	21.6	20.5	20.0	23.4
AMI: L1	4.1	2.9	3.2	3.0	3.2	2.5	3.4	2.7
L2	2.2	3.4	2.6	4.4	4.2	ap	4.4	ar
L3	4.8	ar	2.7	4.1	al	ap	5.0	ar
L4	4.1	4.2	3.9	4.4	4.4	ap	4.5	4.3
R1	2.6	3.2	2.9	2.6	2.8	3.0	3.3	2.5
R2	2.5	3.9	2.8	3.3	3.9	3.8	4.8	ar
R3 (H)	3.1 ar	4.0	3.5	4.8	4.5	ap	4.3	3.3
R4	3.8	4.2	3.8	ar	4.6	3.3	4.9	2.4
AWI	18.2	17.5	23.1	19.2	13.0	14.8	21.4	16.7
ASIn	13.6	12.5	15.4	13.5	9.3	14.8	21.4	16.7
ASIe	22.7	16.7	19.2	23.1	11.1	22.2	32.1	26.7
WDI	12.4	13.9	12.7	10.3	9.6	10.6	13.6	14.1
GC	5	5/6	5	5/6*	5	5	5	5/6
OAI	65.7	ar	128.6	117.8	al	da	85.0	117.6
HASC	89	127	124	134	120	da	115	102
LLI	1.7	2.1	2.1	1.5	1.2	1.5	1.8	2.2
CaLI	18.8	25.0	31.6	21.1	26.7	in	22.7	22.7
SpLI	54.5	41.7	42.3	45.5	35.2	40.7	—	40.0
SpWI	2.1	2.0	2.3	1.9	2.1	2.3	—	2.2
SpRI	33.3	35.0	36.4	32.1	31.6	27.3	—	33.3
FLI	40.9	37.5	42.3	42.3	48.1	48.1	42.9	40.0
FFI	55.6	55.6	63.6	54.5	46.2	46.2	75.0	66.7

*This octopus had only a single, enlarged right gill

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Table 1.3. Measurements (mm) and indices of female *Octopus brachiotomus*, sp. nov. al, arm lost; ar, arm regenerating; da, damaged; im, immature; su, submature; ma, mature; sp, spent; —, not recorded.

Museum Registration Number

Abbreviations as in Appendix I	UGI unreg.	USNM unreg.	UGI[1] unreg.	USNM unreg.	UGI unreg.	USNM 885670 Allotype	BMH unreg.	NMV F80721	UGI[3] unreg.
ML	15	20	22	24	26	26	28	30	33
StM	im	su	sp	sp	su	sp	sp	ma	ma
TL	76	120	140	135	128	158	156	167	163
TWt, g	2.5	6.3	7.7[2]	9.4[2]	7.5	11.0[2]	16.4[2]	19.7	13.7[2]
MWI	60.0	70.0	81.8	66.7	69.2	65.4	67.9	56.7	69.7
HWI	66.7	65.0	59.1	54.2	53.8	50.0	50.0	46.7	45.5
MAI	23.4	20.0	19.3	19.5	23.0	19.3	21.4	19.1	25.2
AMI: L1	3.0	3.5	3.8	3.1	2.8	2.5	ar	3.9	al
L2	3.1	4.4	4.2	3.5	ar	4.6	3.2	4.5	al
L3	4.1	4.3	5.2	4.2	4.0	4.8	4.7	5.0	al
L4	4.3	3.7	5.1	ar	4.1	3.6	3.9	4.0	al
R1	3.2	3.2	3.6	3.1	2.9	2.9	ar	ar	131
R2	3.5	4.0	5.4	4.2	3.4	4.9	3.1	4.6	al
R3	4.1	5.0	4.4	5.1	4.3	5.2	3.6	4.6	al
R4	3.6	ar	5.0	ar	4.0	5.0	4.1	5.2	al
AWI	13.3	20.0	18.2	20.8	15.4	15.4	17.9	16.7	18.2
ASIn	10.0	11.0	13.6	10.4	8.5	11.5	10.7	10.0	9.1
WDI	da	12.0	12.4	13.8	14.2	13.3	13.7	12.7	al
GC	5/6	5/6	5/6	5	6	5/6	5	—	5/5
Egg Length, mm			2.3[5]	2.7[6]		2.3[5]	1.9[5]		2.0[4]
Egg Width, mm			1.0[5]	1.6[6]		1.1[5]	0.8[5]		1.0[4]
Egg number			3000	—		4500	2000		
FLI	26.7	50.0	68.2	45.8	26.9	61.5	42.9	46.7	42.4
FFI	75.0	60.0	53.3	63.6	63.6	62.5	66.7	57.1	71.4

[1] Captured an estimated 2 weeks post settlement, maintained in captivity 151 days through maturation, egg laying, and brooding. (measurements made after brooding).

[2] Spent females had not eaten for 20-30 days, substantially reducing their body weight.

[3] This female was found with only one arm, R1, all other arms autotomized, rendering many measurements incomplete.

[4] Ovarian eggs

[5] Newly deposited eggs

[6] Deposited eggs after 13 days of 20-day development period.

and 155 in females on normal ventral arms; typically 115 suckers on hectocotylized arm of males. Enlarged suckers on male arm pairs 2 and 3, beginning usually 9 suckers from the mouth. Funnel organ W-shaped (Fig. 1.3b). Gill count 5-6 lamellae per demibranch. Ink sac and anal flaps present. Right third arm of mature males hectocotylized. Ligula short, about 2% of arm length in mature males, pointed with an open shallow groove (Fig. 1.3c). Calamus small and pointed, about 25% of ligula length. Spermatophores (Fig. 1.5c) short (11 mm, 37% of ML) produced in high numbers (mean of 93 in 6 males). Eggs (Fig. 1.7) small (about 2 mm long, 0.8 mm wide), deposited in moderate numbers (1200-7000 in seven females). Adult color pattern beige with brown horizontal arm banding and two solid dorsal mantle white spots, one above each eye. Skin sculpture: occasional raised papillae on mantle, especially above eyes and near mantle tip.

Description: Small octopus on intertidal reefs, active during both day and night low tides; autotomy of all arms seen, except the male hectocotylized arm R3 (Ward and Norman, in prep.) Dorsal mantle length to at least 35 mm for males (MLd 28; 19-27-35) and 33 mm for females (MLd 26; 13-25-33). Male total length to at least 195 mm (TL 177; 96-143-195) and weight to at least 24 g (TWt 23.3; 6.8-13.0-24.2). Female total length to at least 210 mm (TL 158; 64-138-210) and weight to at least 26 g (TWt 10.6; 1.1-10.5-26.1). Mantle shape ovoid, occasionally with pixie cap; mantle walls of moderate thickness. Two solid dorsal white spots on dorsal mantle, one above each eye about one-third distance to mantle tip. Stylets present, length approximately one-third ML, width approximately 0.2 mm.

Mantle opening (pallial aperture) wide, typically 1.5 times mantle width and nearly equal to ML (PAI 85.7; 73.2-93.0-131.8). Funnel moderately narrow and thin-walled, nearly half ML (FuLI 42.9; 23.8-47.0-68.8); free portion over half total funnel length (FFI 75.0; 41.7-57.8-80.0). Funnel organ W-shaped (Fig. 1.3b), limbs broad; outer limbs nearly two-thirds length of median limbs (FOI 37.5-60.1-72.7). Funnel organ length half of funnel length (FOLI; 31.8-46.9-75.0).

Head width typically half greatest mantle width (HWI 57.1; 34.1-52.6-72.7). Eyes medium-sized, moderately pronounced.

Arms moderately long, commonly 4-5-times mantle length (MAI 20.0; 14.0-22.6-33.3), and moderately robust (AWI 21.4; 10.0-16.6-28.6). Arms squarish in cross-section, evenly tapered along their lengths. Arms unequal in length, ventral pair usually longest, grading to dorsal pair shortest; AF typically 4=3.2.1.

Arm autotomy occurs typically after sucker 5 or 6 (less frequently after sucker 4, and rarely after sucker 2, 7, and 8.) Non-autotomy breakage occurs at other positions along arms, and regeneration from both conditions is visible on at least one arm of most specimens. Regeneration from autotomy was noted in 21% of collected females (n=24) and 22% of males (n=37). No scar is visible on nearly or completely regenerated arms, making this estimate of autotomy frequency conservative.

Normal sucker size moderate (male ASIn of L3 19.6; 8.3-13.2-19.6); female largest sucker diameter typically 25-30% less than male largest normal sucker diameter (female ASIn of L3 11.5; 6.3-9.9-13.8). Mature males show 3-5 distinctly enlarged suckers near arm bases (typically suckers 9-11) on arm pairs II and III, occasionally on one or both arms of pair IV, and rarely on one or both arms of pair I. Male greatest enlarged sucker

diameter is nearly twice normal sucker size (ASIe 32.1; 11.1-21.1-32.1). Enlarged suckers are raised above normal suckers one-fourth to one-half diameter of enlarged sucker. Based on two immature males, enlarged suckers appear later in development than R3 hectocotylization. Sucker depth approximately half sucker diameter; suckers typically with 20 septa. Sucker rims finely scalloped. Sucker count generally decreases slightly with decrease in arm length, and in males averages 145 suckers on each arm of pair IV and on L3, 132 on each arm of pair II, 120 on each arm of pair I, and 116 on the hectocotylized arm R3. Females average 12% more suckers than males for the same arm length.

Webs moderately shallow (WDI 13.6; 9.0-13.4-20.4); dorso-lateral and ventro-lateral webs deepest, ventral and dorsal webs shallowest. Female WF typically C=D.B=E.A, males typically D.C.B=E.A; webs on both sides of hectocotylized R3 shallower than corresponding left side webs. Web margins extend as retractable membranes on ventro-lateral arm edges only, for approximately three-fourths arm length.

Third right arm of males hectocotylized, of moderate length (HAMI 425.0; 244.8-359.7-484.6). Arm R3 in males characteristically 10% shorter than opposite arm L3 (OAI 85.0; 62.8-91.0-129.2). Spermatophore groove well developed, wide and thin with fine transverse ridges. Ligula narrow and short in mature males (LLI 1.8; 1.2-2.1-3.0), cylindrical, tapering to blunt point (Fig. 1.3c). Ligula groove moderately deep. Calamus small, often indistinct (CaLI 27.3; 15.0-24.2-34.3) with narrow spermatophore guide. Approximately 115 suckers on hectocotylized arm (HASC 115; 82-116-134).

Gills with 5-6 lamellae on both inner and outer demibranchs.

Two anal flaps present.

Beaks as illustrated in Fig. 1.4. Upper beak (Fig. 1.4a) with a short hooked rostrum and narrow hood. Lower beak (Fig. 1.4b) with moderately sharp rostrum, narrow hood, moderately spread wing and flared lower lateral walls. Radula (Fig. 1.4c) with seven teeth.

Male genitalia as illustrated in Fig. 1.5. Spermatophores (Fig. 1.5c) short (SpLI 35.2-54.5, n=7) and narrow (SpWI 1.9-2.3, n=7), produced in moderate numbers (approximately 40 to 160 in Needham's Sac of 6 males). Oral cap simple with 1-2 mm cap thread. Sperm reservoir approximately one-third spermatophore length (SpRI 31.6-36.4, n=6).

Female genitalia as illustrated in Fig. 1.6. Four gravid and seven egg-depositing females were examined. Mature ovarian eggs small, capsule length to 2.7 mm, width to 1.1 mm (n=4 females); newly deposited egg length to 2.4 mm (EgLI 7.9), width to 0.9 mm (EgWI 3.1); embryonic capsule just prior to hatching to at least 3 mm long and 1.3 mm wide. Eggs produced in moderate numbers; numbers of eggs deposited in captivity ranged from approximately 1200 for a small female (ML 20) to 8000 for a moderately large female (ML 32).

Embryonic development time is 19-20 days at ambient seawater temperature of 27-28° C. Eggs are arranged in egg chains, typically about 100 eggs per 30 mm chain (Fig. 1.7), though as few as 44 and as many as 147 eggs were recorded on chains from 15 mm to 51 mm in length. Number of egg chains deposited by females ranged from 36 to 80 (n=6).
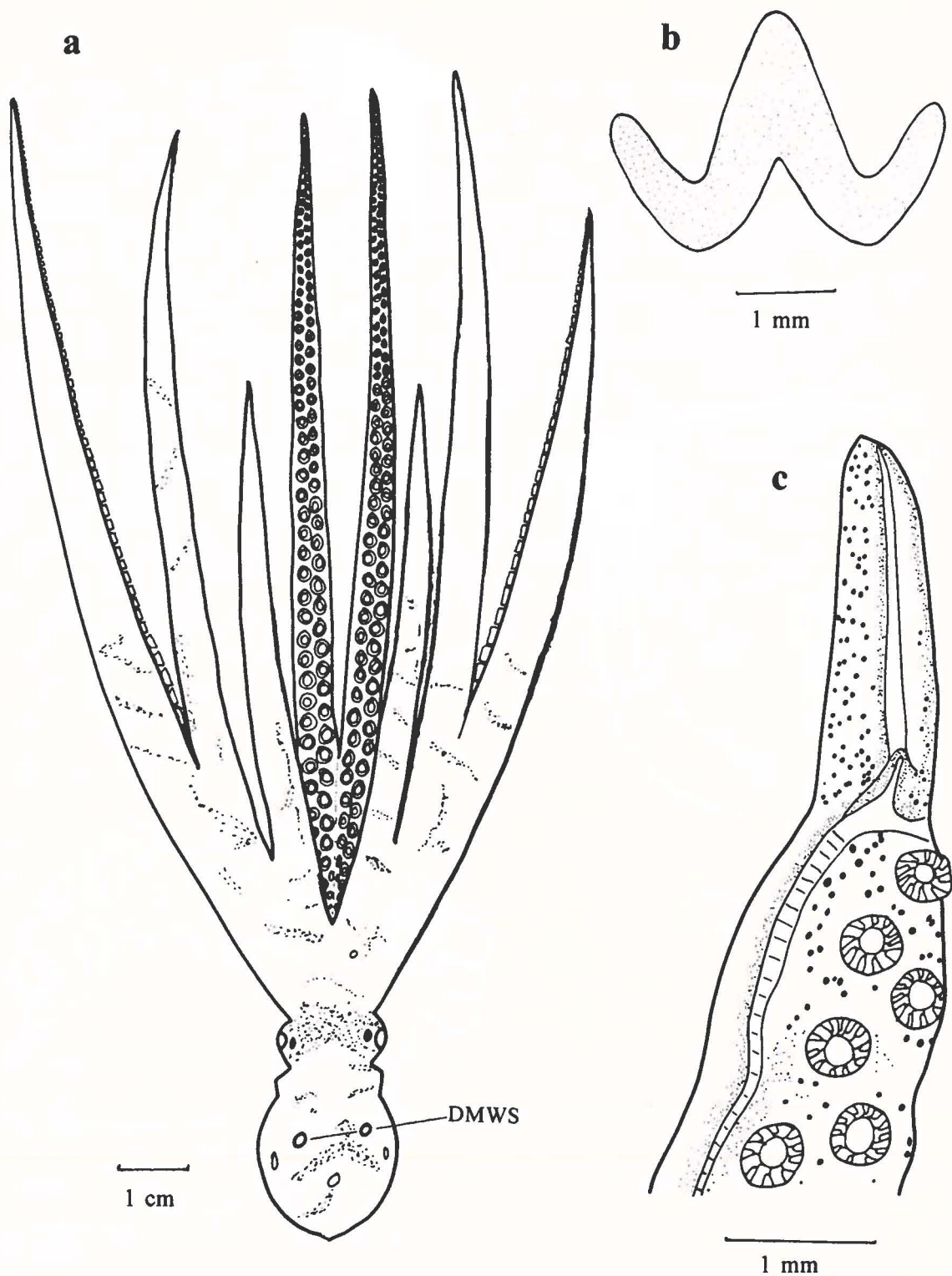
Figure 1.3. *Octopus brachiotomus*, sp. nov. *a*, dorsal view of 28 mm ML ♂ holotype (USNM 885669): **DMWS** = dorsal mantle white spots. *b*, funnel organ of 22 mm ML ♂ (UGI unreg.). *c*, hectocotylized arm of 28 mm ML ♂ (CASIZ unreg.).
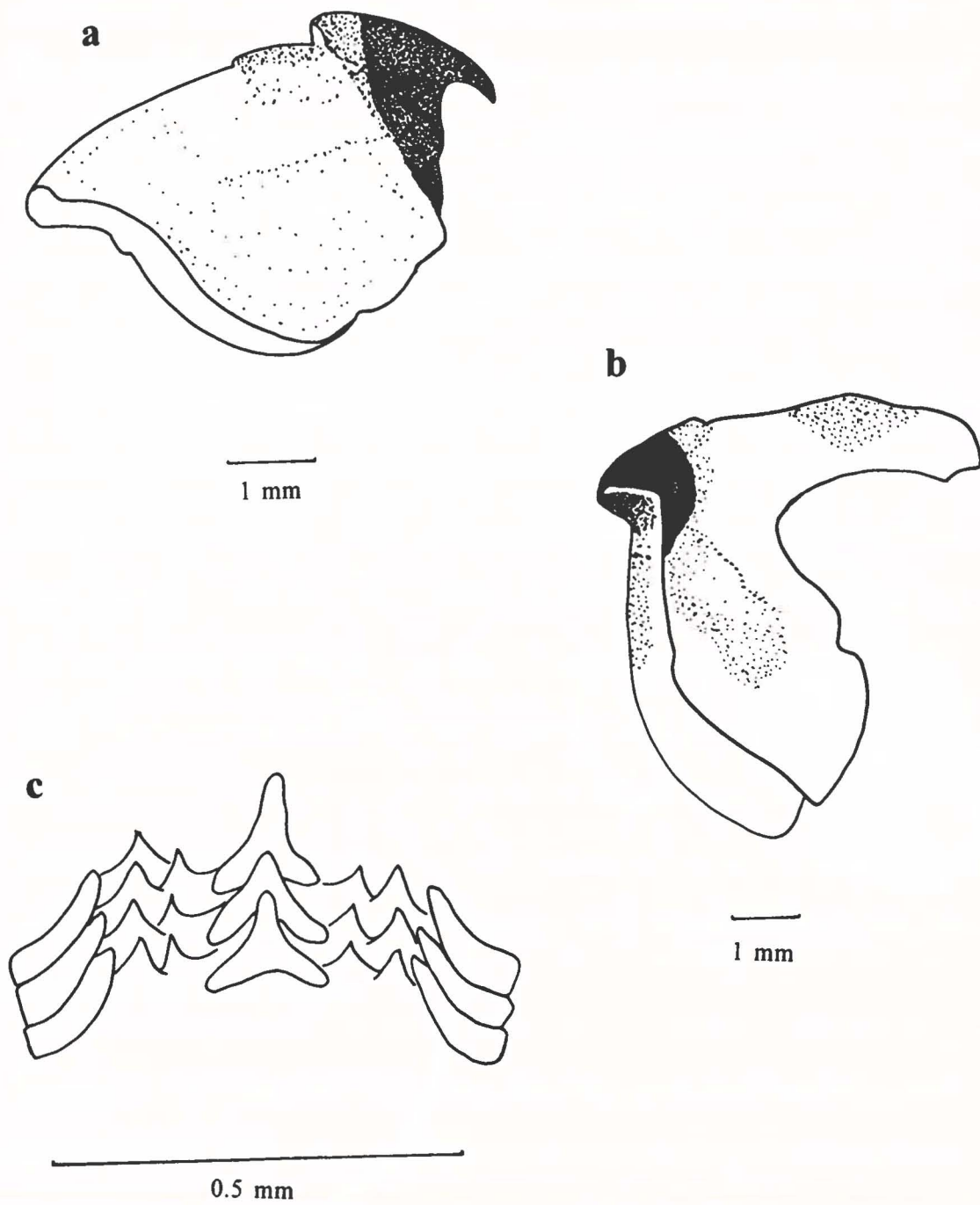
Figure 1.4. *Octopus brachiotomus*, sp. nov. *a*, Upper beak of 26 mm ML ♂ (UGI unreg.). *b*, Lower beak of same animal. *c*, Radula of 25 mm ML ♀ (UGI unreg.).
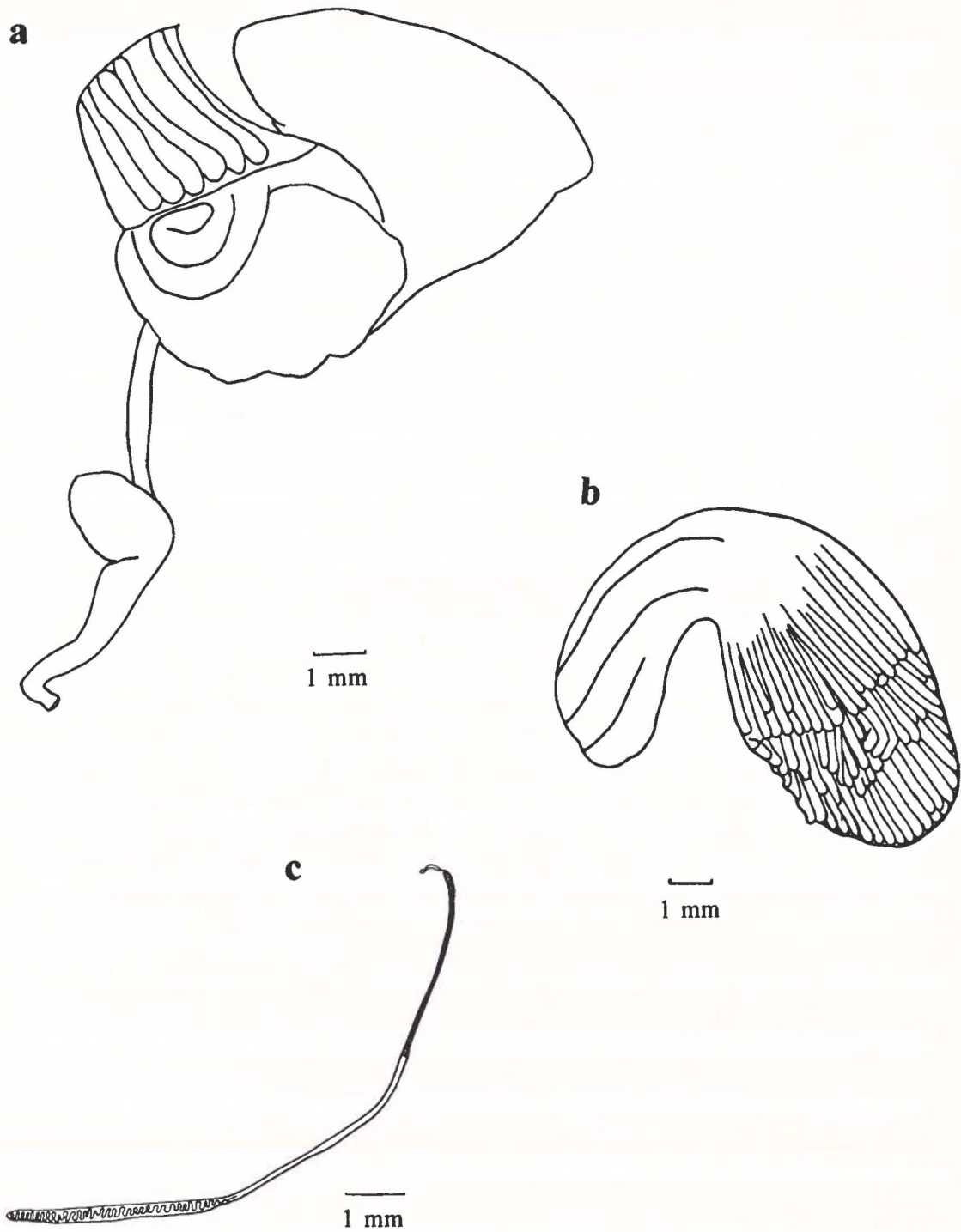
Figure 1.5. *Octopus brachiotomus*, sp. nov. *a*, Male reproductive system of 30 mm ML ♂ (SBMNH unreg.). *b*, Spermatophore sac (Needham's sac) of same animal. *c*. Spermatophore of same animal.

Hatchlings TL about 2.6 mm, MW about 1.1 mm, subequal arm lengths about 0.7 mm. Arms with 3 uniserial suckers. Four dorsal arm chromatophores in 2 rows plus large arm base chromatophore (Fig. 1.6c). Dorsal head chromatophores 2+2+4. Mantle flask shaped. Dorsal mantle with few (11) large chromatophores. Funnel with 2 small chromatophores (Fig. 1.6d). Ventral mantle with many (26) large chromatophores in 6 rows: 5, 6, 6, 4, 3, 2 across.

Body coloration variable. Base color usually cream with a series of mottled auburn-brown horizontal arm stripes extending across webbing, with corresponding mottled pattern on head and mantle. Paired, elliptical, solid white spots are evident on dorsal mantle, one above each eye, approximately one-third distance from eye to mantle tip (Fig. 1.8). Animals also blanch to unpatterned base color and darken to unpatterned auburn brown. Only one animal was seen to exhibit a lateral bicolor arrangement, a pattern typical of *O. cyanea*, (pers. obs.), in which the left side of the mantle, head, and arm crown are darkened, and the right side lightened, or *vice versa*. Characteristic skin texture is smooth, but raised papillae over mantle, head, and arm dorsal surfaces often accompany skin color changes.

Remarks: The characteristic two dorsal mantle white spots, one located above each eye, are typically visible in preserved specimens. Sexual dimorphism is apparent in mature animals: enlarged suckers are present on arm pairs 2 and 3 of males as small as 19 mm ML.

Distribution: Though this description includes specimens from Guam only, the animal's reproductive mode: production of many small eggs which hatch into pelagic larvae, suggests a potentially broader distribution.

Life History: A tiny female (TL approximately 20 mm, ML approximately 7 mm) found under a rock in the intertidal zone in mid-May was maintained in captivity through maturation, egg-laying, and brooding in mid-October (22 weeks). When found and for six weeks thereafter, the animal's coloration was an even brick-red; its skin texture quite smooth. Unlike typical adults of this species, it inked frequently, often 5-7 times in succession. Arm pair I was shortest in length at time of capture, and remained so throughout life.

Nineteen days after capture, as its container was being routinely cleaned, the tiny octopus autotomized arm R1, only 12 mm in length at the time. Within 8 weeks the arm had completely regenerated. By six weeks after capture, the small octopus' skin coloration had changed from an even brick red to a beige background with tiny deep-brown arm speckles; the distinctive two dorsal white spots on the mantle, one above each eye became apparent. The first clue to the sex of this small octopus was she did not especially protect arm R3 from touch even after the 14th week.

In the first month the tiny octopus ate an average of 1.2 crabs (3-5 mm carapace width) per day. From weeks 11 to 19 her daily crab (7-10 mm carapace) intake increased, leveled off, then decreased to zero, averaging: 3.8, 4.3, 6.4, 6.4, 5.5, 5.0, 4.0, 3.3, 0.4. By week 17 of captivity her mantle was distended and yellow with ova. In week 19, although she had not been in contact with a male during captivity, she ceased eating and began to deposit eggs. On the second day of egg deposition the female was

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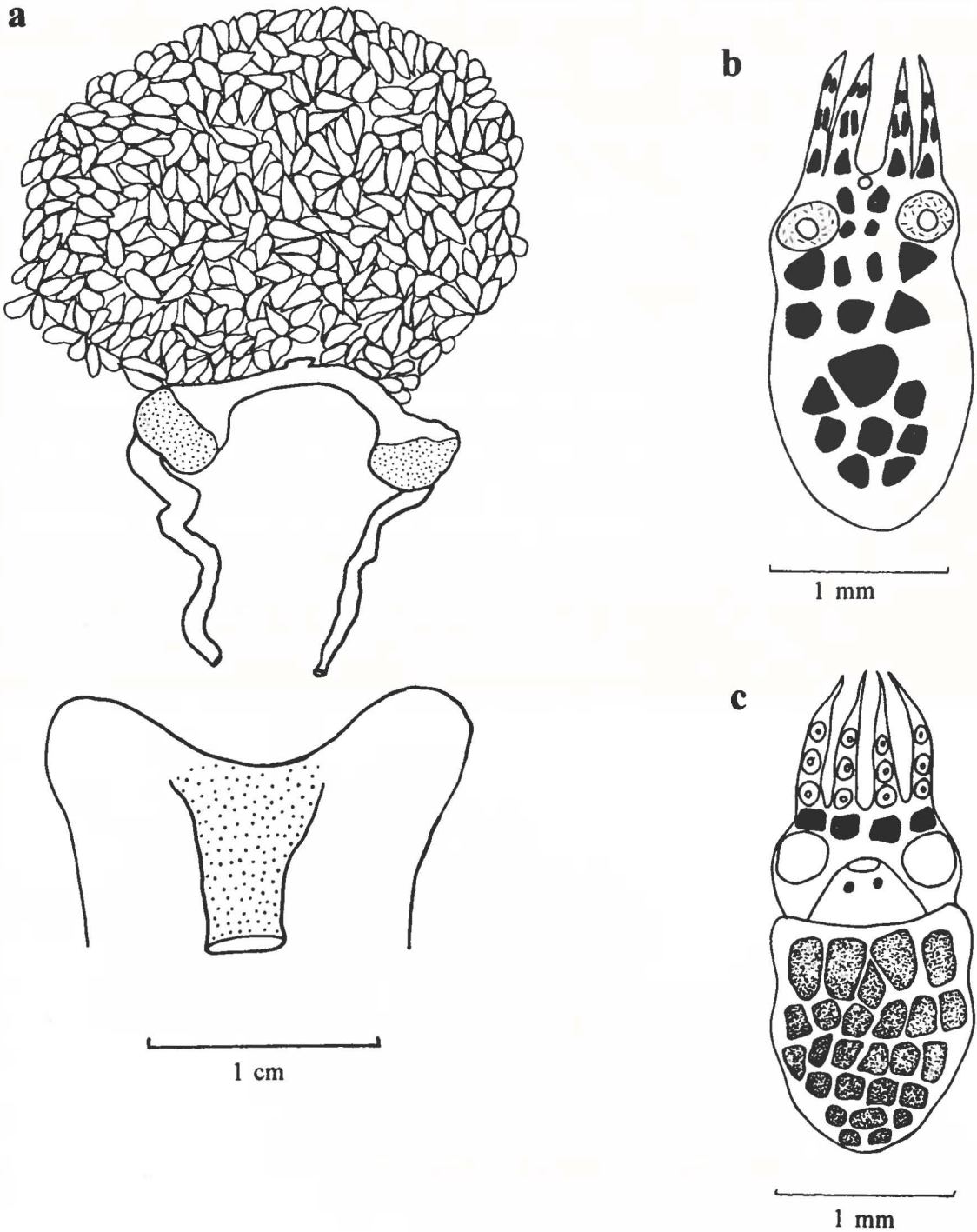
Figure 1.6. *Octopus brachiotomus*, sp. nov. *a*, Female reproductive system of 20 mm ML ♀ (USNM unreg.). *b*, Hatchling, dorsal, of 26 mm ML allotype ♀ (USNM 885670) showing only arm pairs I and II. *c*, Same hatchling, ventral, showing only arm pairs I and II.

placed with 3 mature males in turn. She approached the first male; he readily extended his hectocotylized R3 arm into the female's mantle cavity. The female then moved steadily around the tank, seemingly pulling the male after her by his extended arm. This mating behavior lasted approximately 20 minutes, after which time the female rejected further mating attempts. The female rejected mating attempts by the second and third males as well. Eggs deposited by the female subsequent to the mating were fertilized, and hatched 20 days later; the infertilized eggs deteriorated. I recorded similar, though more extended, mating behavior of a different male and female pair in which the female repeatedly moved ahead of the male, apparently pulling him by his extended hectocotylized arm, has also been recorded.

Figure 1.7. *Octopus brachiotomus*, sp. nov. Egg chain of 28 mm ML ♀ (BMH unreg.).

Figure 1.8. *Octopus brachiotomus*, sp. nov., showing paired dorsal mantle white spots.

Females characteristically double or triple their food intake for 3-4 weeks just prior to oviposition, then stop eating entirely for 1-5 days prior to egg deposition, which extends over 3-4 days. At least a few days prior to egg laying, with mantles distended with yellow ova (Fig. 1.9), females develop dark eye rims, usually in conjunction with a dark overall body coloration. Eleven females in captivity deposited eggs in six different months (January, February, April, May, August, September); although confinement may have accelerated this process, there is no evidence of a specific spawning period in this species. Egg strings are attached to a rigid surface; in captivity females attached strings to bricks, plastic container walls (Fig. 1.10), large bivalve shells, and fiberglass tank walls. Females offered food during brooding refused it, continually cradled and

Figure 1.9. *Octopus brachiotomus*, sp. nov. 29 mm ML ♀ (UGI unreg.) showing mantle distended with yellow ova.

groomed their eggs, underwent senescence, and died 3-6 days after the last eggs hatched. Removal of the empty egg case mass after hatching appeared to hasten death in spent females; one female exhibited multiple arm autotomy, another, multiple arm autophagy within 24 hours of empty egg mass removal.

Hatchlings characteristically show the melanophore pattern in Fig. 1.6a, b. Arms are approximately equal in length at hatching, with three uniserial suckers each. Hatchlings are active swimmers, moving about by jetting; they apparently remain planktonic for an unknown period before settling to a benthic lifestyle.
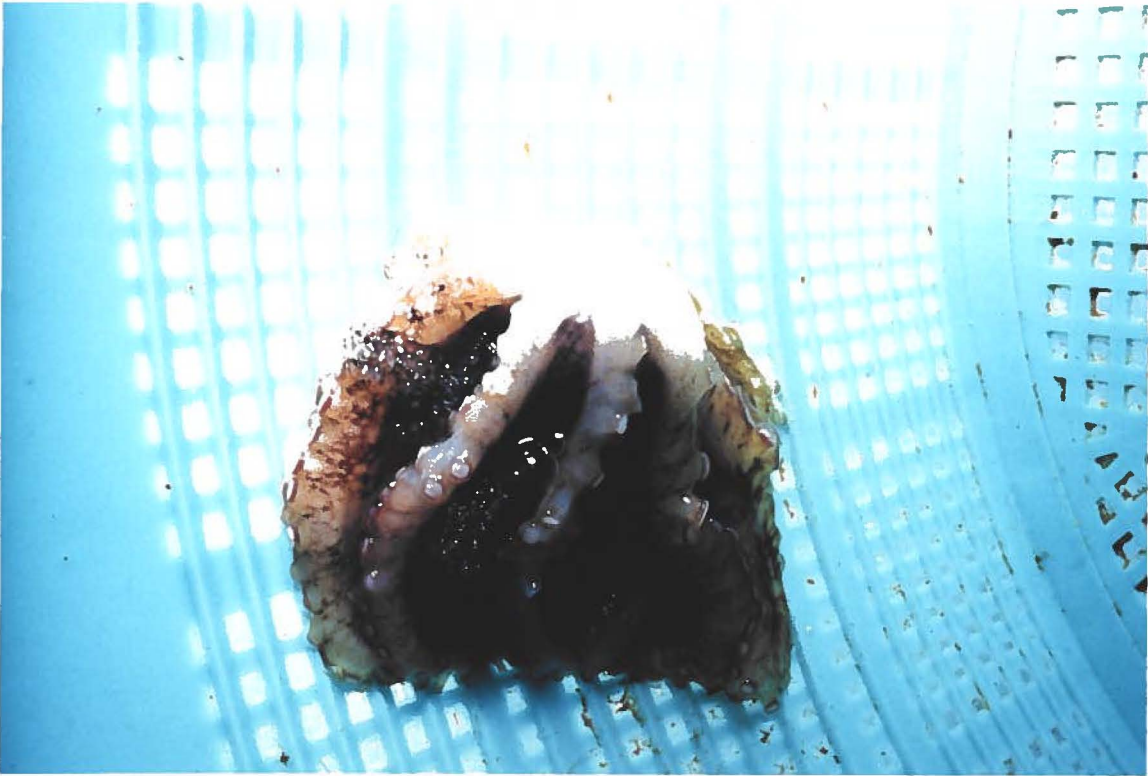
Figure 1.10. *Octopus brachiotomus*, sp. nov. 22 mm ML ♀ (UGI unreg.) brooding eggs.

Lifespan of this species is unknown but can be roughly estimated from laboratory data. The approximately 20 mm TL female kept through maturation, egg deposition and hatching, and senescence lived in captivity 22 weeks. The egg development period is known to be 19-20 days or roughly 3-weeks. Newly-settled *O. cyanea*, one of the larger tropical octopods, were described by Wells and Wells (1970) as "about 1 cm long, head and body, arm-span of 2-3 cm when fully extended". This size roughly corresponds with the 2 cm TL juvenile. If *O. brachiotomus* is smaller at settlement than its much larger congener (which deposits 50% larger (3 mm) eggs), then the 2 cm captured animal may have been a few weeks post-settlement. The planktonic stage of *O. vulgaris* (which hatch from eggs the same size at oviposition, 2 X 1 mm, as this small species, is

given by Itami et al. (1963 in Van Heukelem 1983) as 30-40 days; a similar period is proposed for *O. cyanea* by Van Heukelem (1983). Assuming a slightly shorter planktonic period of 4 weeks for a species in warmer water, total life span for a female fed *ad libitum* in captivity may have been approximately 30-33 weeks. Natural life span may be somewhat longer if food is not abundantly available, limiting growth and the rate at which gametes can be produced.

One female with a mantle necrosis found on the reef flat during a summer noon low tide had seven arms autotomized; only R1 remained (Fig. 1.11). As she refused food and appeared to degenerate in captivity; she was preserved a few days after capture. Dissection revealed her ovary to be full of mature eggs. S. Seino (University of Tokyo,

Figure 1.11. *Octopus brachiotomus*, sp. nov. 33 mm ML ♀ (UGI unreg.) found with mantle injury and 7 arms autotomized.

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pers. comm.) described how *Octopus vulgaris* females place eggs individually from the funnel into the first row of suckers, called 'egg suckers,' around the mouth, and there manipulate each egg in turn into a growing egg string. If the mechanism of egg deposition in this species is similar, a one-armed female could theoretically still have produced egg strings with the 'egg suckers' of the autotomized arm stubs, and deposited the egg strings if she were able to sufficiently anchor herself with her one complete arm. Such extreme autotomy behavior could, however, reduce a semelparous female's fitness to zero.

The individuals longest in captivity, aside from the newly-settled female, were four males captured at adult size, kept 13, 14, 15, and 16 weeks. Two of these males were killed and preserved, one after his body color had turned dark, his food intake decreased from 1 to 1/2 crab per day for 10 days, and 4 arms, including the hectocotylized R3, were reduced to 1/3 - 1/2 their former lengths, apparently of autophagy. Two males died, one of insufficient water flow, the other apparently of natural senescence, after his body turned dark in color, his movements slowed considerably, and he refused all food for 10 days.

Natural History: Diet of this octopus in captivity was almost exclusively intertidal grapsid and xanthid crabs, though some individuals occasionally ate the small mussel *Modiolus auriculatus* or small *Gafrarium pectinatum* clams, and infrequently the fragile bivalve *Isognomon perna*. One captive octopus ate part of a freshly-killed small apogonid (squirrel fish). The intertidal toxic (Inoue et al. 1968) xanthid crab, *Atergatis floridus*, was nearly always refused (though larger of these crabs were readily eaten by a captive *Octopus cyanea*). Freshly killed penaeid shrimp tails were occasionally given to

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the animals; some ate them; others did not. On one occasion, whole, freshly-killed 7 cm penaeid shrimp were given to 10 octopuses; in less than 24 hr 3 octopuses had died, apparently from ingesting the shrimp.

No drill holes were apparent on any crab carapaces or bivalve eaten by this small octopus. Mussel shells were apparently flexible enough to allow access between the distal edges; rigid bivalves were bitten along the distal edge, or crushed if very small.

A few captured octopuses were holding 3-4 grapsid crabs under their webs as they moved about the intertidal zone; most, however, did not carry food. Others were found eating *Actaeodes tomentosus* and other xanthid crabs. No semi-permanent lairs of this species were identified, perhaps because carapaces of the small crab prey would be easily scattered by tidal action, eliminating a major visual cue of other, e.g. *Octopus cyanea*, dens. This octopus is sufficiently small and slender to quickly find temporary refuge nearly anywhere on the reef flat, is additionally protected by its capacity for arm autotomy, and may not establish dens as such.

Although I spent more time searching the intertidal immediately following low tide, nearly twice as many of these octopuses were encountered just prior to the tide change. Apparently this small octopus is more active at times when most fish predators have left the reef in anticipation of falling water levels. It is well-known by fishermen that fish feed at the rising, rather than at the falling tide. At night, however, small eels which are recognized octopus predators, were present in even shallow intertidal waters.

Discussion

The small littoral octopus described here is commonly referred to on Guam as *gamsom dikike'* or "baby octopus," by local Chamorro fishermen. This animal is not generally taken for food or bait, though its larger congener, *Octopus cyanea* is a prized catch, often captured at low tide by wading or snorkeling fishermen who probe suspected intertidal and shallow-water octopus lairs with wire until a harassed animal emerges.

The species treated here is described as a new member of the *Octopus horridus* group (Norman 1993a, Norman and Sweeney 1997). Members of this group typically occur on intertidal coral or rocky reefs, active in shallow ponds during day low tides. Norman and Sweeney (1997) discuss this group, describing one new member species from the Philippines. Diagnostic characters for this group are:

•Small to moderate size (<70 mm ML)

•Elongate arms (3.5-7 times ML) capable of autotomy at a set level near the arm base

•Lateral arms and webs longer/deeper than dorsal ones

•Small narrow ligula (<5% of hectocotylized arm length)

•Enlarged suckers on arm pairs II and III in mature males

•Low to moderate gill counts (5 to 8 per demibranch)

•Full set of "dorsal white spots" and "frontal white spots" *(sensu* Packard and Sanders 1971)

•Multiple primary and secondary papillae on the mantle, arm crown and arms, capable of being raised as plain or branched digits. These papillae are employed in accurate camouflage against algae and coral backgrounds.

The taxonomy of this species group is poor, due partly to problems associated with an attribute of this species group, arm autotomy. Partial regeneration of autotomized arms confuses the ordering of relative arm lengths, an important diagnostic character in

octopus taxonomy. Due to inadequate original descriptions, the status of many species remain uncertain.

Norman (pers. comm.) has noted that *Octopus defilippi* of the Mediterranean Sea and Atlantic Ocean shows superfical similarities with the *Octopus horridus* group, namely similar body size and long arms capable of autotomy. As Norman notes, however, *O. defilippi* is distinct in a number of attributes:

• Enlarged suckers are absent in both sexes

• "Dorsal white spots" and "frontal white spots" *(sensu* Packard and Sanders 1971) are absent.

• Gill counts are relatively higher (9-10 gill lamellae per demibranch).
  This species group derives its name from *Octopus horridus*, described from the Red Sea. *O. horridus* is distinct from the new species treated here in that it produces large eggs in low numbers, and possesses a larger ligula and many more enlarged suckers in mature males (Norman pers. comm.). The genuine *Octopus horridus* is restricted to the Red Sea and Western Indian Ocean; however the species name has been used widely in the literature for members of the species group throughout the tropical Indian and Pacific Oceans (Norman, pers. comm.). *Octopus brachiotomus* is distinguished from other members of this species group in Table 1.4, including two undescribed species reported from the Great Barrier Reef by Norman (1993a) and one undescribed species reported from the Philippines by Norman and Sweeney (1997).

The *Octopus horridus* group is known only from the tropical and warm temperate waters of the Indo-West Pacific region, from Hawaii to the Red Sea, and southern Japan to South Africa. This distribution, coupled with the highest number of member species occurring in the Indo-Malayan Archipelago, suggest either a relatively recent origin and radiation of this species group throughout the shallow warm waters of the Indo-Pacific

Table 1.4. **Comparison of** *Octopus brachiotomus*, **sp. nov., with 10 of the 16 other members of the** *Octopus horridus* **species group for which data are available** (Norman pers. comm., Norman and Sweeney 1997).

Abbreviations as in Appendix I

Species	GC	HASC	Enlarged Suckers Number	Position	♂ ASI	AMI	Autotomy proximal sucker	LLI	OAI	WDI	SpLI	Egg size
Octopus brachiotomus	5-6	80-134	2-4	8-11th	♂ 13.2 ♀ 10.2	3.6-5.4	4-7th	1.2-2.8	63-98	9-20	35-55	small
Octopus abaculus	6	90-120	8-12	10th+	♂ 14.2 ♀ 12.5	4.5-6	5-8th	3.8-6.4	59-74	8.7	11.8	small
Octopus aculeatus	6-7	138-175	5-12	11th+	♂ 18.2 ♀ 8.9	5-6	5-8th	1.5-1.8	73-83	9-12	15-19, 39-57	small
Octopus harmandi	6	152	4-5	11th+	♂ 18.9 ♀ 16.5	6.0-6.6	—	1.8	<83	10.2	—	small
Octopus horridus	5-6	90-94	10-18	11th+	♂ 23.7 ♀ —	4.2-4.7	7-10th	3.1-4.0	67-75	14.8	12.8, 64.6	large
Octopus mutilans	7-8	52-72	not obvious		♂ 9.4 ♀ 7.5	6.0-7.6	varies	3.0	~50	6-7	22, 45.8	unknown
Octopus tenebricus	7	93	not obvious		8.2 - 9.3	3.2-3.8	—	4.4	87.2	13.6, 17.8	7.5, 46.5	large
Octopus tonganus	6	129	2-3	8th+	♂ 29.5 ♀ 10.4	8.1	6-7th	1.1	71.0	11.8	—	small
Octopus sp. 1 Norman, 1993	7	152-166	2-3	9-11th	♂ 17.8 ♀ 11.1	4.9-6.7	4-5th	1.4-2.3	—	11.7-15.6	21, 51-55	small
Octopus sp. 2 Norman, 1993	7	117-137	2-3	8-12th	♂ 24.6 ♀ —	4.0-5.0	3-7th	2.3-3.0	78-82	14.2-18.4	11.5, 28.8	small
Octopus sp. 2 Norman & Sweeney, 1997	6-7	105-125	1	8th	♂ 22.9 ♀ —	4.3-4.7	2-5th	1.8-2.3	—	16.5-19.6	40.9-42.2	—

region (Norman pers. comm.) or extinction of the group from other ocean basins, as with scleractinian coral genera (Paulay 1997).

Terminology

Calamus: Small tongue-like projection at the base of the ligula (modified tip) of the hectocotylized arm of males.

Funnel organ: Distinctive patch (or patches) of glandular tissue present on the inner walls of the funnel, exposed by dissection of the funnel along the ventral midline.

Hectocotylus/Hectocotylized arm: Modified arm in males which transfers spermatophores into the oviducts of females.

Ligula: Club or spoon-like modified tip of the hectocotylized arm of males.

Spermatophore groove: Channel or gutter along the ventral edge of the hectocotylized arm, often lined with transverse creases.

Spermatophore guide: Crease or grip at base of the hectocotylized arm which receives and guides spermatophores into the spermatophore groove.

Spermatophores: Complex hair- to rod-like coated structures used to transfer sperm to the females. Each consists of a sperm reservoir (containing the coiled sperm cord) and an ejaculatory apparatus (which everts the structure to form a sperm bulb).

Stylets: Rod-like inclusions in the dorsal mantle of many octopuses, considered the vestigial shell of shelled ancestors.

Definitions of counts, measurements (in mm), and indices
(Roper et al. 1983, Norman 1993a)

Arm Formula (AF): comparative length of arms expressed numerically in decreasing order (e.g., III.IV=II.I. indicates arm pair III>IV=II>I).

Arm Mantle Index (AMI): arm length as a percentage of mantle length. (Arm I, dorsal; II, dorso-lateral; III, ventro-lateral; IV, ventral).

Arm Sucker Index (ASIn): diameter of largest normal arm sucker on each designated arm as a percentage of mantle length.
(ASIe): diameter of largest enlarged arm sucker (arm designated) as a percentage of mantle length.

Arm Width Index (AWI): arm width at widest point on stoutest arm as a percentage of mantle length (measurement exclusive of webs and membranes).

Calamus Length Index (CaLI): length of calamus measured from last (distal-most) sucker to its distal tip as a percentage of ligula length.

Egg Length Index (EgLI): length of mature egg as a percentage of mantle length (use spawned eggs if available, otherwise from the oviduct).

Egg Width Index (EgWI): greatest width of mature egg as a percentage of mantle length (use spawned eggs if available, otherwise from the oviduct).

Funnel Length Index (FLI): length of the funnel from the anterior funnel opening to the posterior border measured along the ventral midline, as a percentage of mantle length.

Free Funnel Index (FFI): length of the funnel from the anterior opening to the point of dorsal attachment to the head as a percentage of funnel length.

Funnel Organ Index (FOI): length of outer limb of funnel organ as a percentage of medial limb length.

Funnel Organ Length Index (FOLI): length of medial limb of funnel organ as a percentage of funnel length.

Gill Count (GC): number of gill lamellae per demibranch not including the terminal lamella.

Head Width Index (HWI): greatest width of head at level of eyes as a percentage of mantle length.

Hectocotylized Arm Mantle Index (HAMI): length of hectocotylized arm as a percentage of mantle length.

Hectocotylized arm sucker count (HASC): number of suckers on hectocotylized arm.

Ligula Length Index (LLI): length of ligula measured from distal-most sucker to tip of arm as a percentage of hectocotylized arm length.

Mantle Arm Index (MAI): mantle length as a percentage of longest arm length.

Mantle Length (ML): dorsal mantle length measured from midpoint between eyes to posterior end of mantle.

Mantle Width (MW): greatest straight-line dorsal width of mantle.

Mantle Width Index (MWI): greatest dorsal straight-line width of mantle as a percentage of mantle length.

Opposite Arm Index (OAI): length of hectocotylized arm as a percentage of its fellow arm on opposite side.

Pallial Aperture Index (PAI): the measurement between the points of attachment of the mantle to the head along the ventral margin of the mantle as a percentage of mantle length.

Sperm Reservoir Index (SpRI): length of sperm reservoir as a percentage of total spermatophore length.

Spermatophore Length Index (SpLI): length of spermatophore as a percentage of mantle length.

Stage of Maturity (StM): Immature (Imm: sex indeterminate or reproductive organs minute), Submature (S: reproductive organs distinct but poorly developed), and Mature (M: developed eggs or spermatophores distinct).

Spermatophore Length Index (SpLI): length of spermatophore as a percentage of mantle length.

Sperm Reservoir Index (SpRI): length of sperm reservoir portion of spermatophore as a percentage of spermatophore length.

Spermatophore Width Index (SpWI): greatest width of spermatophore as a percentage of spermatophore length.

Sucker Count (SC): number of suckers on arm with highest sucker count.

Total Length (TL): distance from end of longest arm to posterior end of mantle.

Total Weight (TWt): weight in g of the octopus, including any unregenerated autotomized arms.

Web Depth Index (WDI): measurement of deepest (most extensive) sector of web measured from mouth to midpoint of sector between arms as a percentage of longest arm. (Web sector A: dorsal to dorsal arm; B: dorsal to dorso-lateral; C: dorso-lateral to ventro-lateral; D: ventro-lateral to ventral; E: ventral to ventral.)

Web Formula (WF): comparative depth of each web sector measured from mouth to midpoint of sector between arms, expressed alphabetically, in decreasing order (e.g., B.C.D=A.E indicates web B>C>D=A>E).

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Chapter 2

Arm autotomy in a small littoral octopus from Guam

An undescribed species of small, shallow-water octopus from Guam exhibits arm autotomy. Loss of the hectocotylized right third arm of males used for sperm transfer could significantly reduce fitness of the semelparous male, depending on arm regeneration time. Enlarged suckers on the males of some species have been suggested to play roles in mate attraction or detection and to provide heightened chemosensitivity of receptive females. Tests of autotomy showed that the hectocotylized male arm is preserved from autotomy, but arms bearing enlarged suckers are not preserved from autotomy. Regeneration from autotomy was found in approximately 20% of animals in the field, while regeneration from other causes occurred in over twice as many individuals. Arms completely regenerated from autotomy in approximately 10 weeks, as measured on captive animals. Incidence of arm autophagy was noted in animals held through to senescence. No plane of weakness or mechanism of autotomy was found by histological examination, using light microscopy, of the arm autotomy zone.

Introduction

An undescribed species of small, shallow-water octopus from Guam (Ward and Norman, in prep.) exhibits arm autotomy. This species, *Octopus brachiotomus*, belongs in the *Octopus horridus* species group as defined by Norman (1993a, Norman and Sweeney 1997). The species in this group of small to medium-sized, shallow water octopuses have elongate arms, well-developed cryptic color patterns and sculpture. Members of the group are primarily day-active, emerging to forage on intertidal coral and rocky reefs during periods of low tide. Members of the *O. horridus* group are capable of arm autotomy and subsequent arm regeneration. The arm separation at autotomy occurs rapidly at the arm bases and appears, at least in part, to be behaviorally controlled. Detached arms are active, coiling and moving along surfaces by means of sucker attachment. Their chromatophores are also active, producing changes in pattern and color along the moving arms.

Autotomy, defined by Wood and Wood (1932) as the reflex severance of a limb or other body part at a preformed breakage plane, is known in the plant kingdom and in

several animal phyla including cnidarians, annelids, molluscs, arthropods, echinoderms, and chordates. Reports include decapods (Wood and Wood 1932, Hoadley 1937, McVean 1976), arachnids (Wood 1926, Eisner and Camazine 1983, Roth and Roth 1984, Formanowicz 1990), lepidopterans (Moore and Tabashnik 1989, Moore et al. 1989), asteroids (Anderson 1956, Davis 1967, Mladenov et al. 1989), ophiuroids (Wilkie 1978a, Bowmer and Keegan 1983, Dobson 1985), lizards (Clark 1971, Congdon et al. 1974, Vitt et al. 1977, Jaksic and Fuentes 1980, Dial and Fitzpatrick 1983, Daniels 1985a, b), salamanders (Maiorana 1977, Houck 1982, Beneski 1989) and mice (Layne 1972). In molluscs autotomy is known to occur in four of the seven living classes: gastropods, bivalves, scaphopods, and cephalopods (Stasek 1967).

The casting off of body structures is a strategy used as defense against predation, entrapment, toxicity accumulation, and as a means of achieving fission (Emson and Wilkie 1980). Release of a structure under attack primarily facilitates escape (Congdon et al. 1974, Dial and Fitzpatrick 1983). Sustained movement of the autotomized structure may have a secondary function, to distract a predator from the escaping prey and/or attack and ingestion of the released body part may allow more time for escape (Dial and Fitzpatrick 1983, Labanick 1984). "Attack autotomy" has also been described (Robinson et al. 1970) in freshwater and terrestrial crabs which attach a pinching chela to an attacker, autotomize the cheliped (which had not been injured or attacked), and retreat.

Molluscan body parts which can be autotomized include the posterior portion of the foot in some prosobranchs (Fishelson and Qidron-Lazar 1966), opisthobranchs (Di Marzo et al. 1993) and pulmonates (Pakarinen 1994, Deyrup-Olsen et al. 1986); cerata, papillae or mantle margins in several opisthobranchs (Edmunds 1974, Marin et al. 1991); mantle tentacles, siphons, or foot tip in some bivalves (Hodgson 1984); feeding filaments in some scaphopods (Stasek 1967); female dorsal arms and the male

hectocotylized arm of argonautoids (J.M. Arnold 1984); and arms in a number of benthic octopuses.

Autotomy in the Octopoda has been described for only three genera of pelagic octopods: *Tremoctopus, Ocythoe*, and *Argonauta* (Stasek 1967, Roper and Sweeney 1975), and for members of the Octopodidae listed in Table 2.1.

In the Octopodidae, autotomy appears restricted to long-arm species that occur in tropical and sub-tropical waters (Norman 1993a), including all 13 described and 3 undescribed species of the *O. horridus* species group (Table 2.1) as defined by Norman (1993a) and Norman and Sweeney (1997).

Octopus brachiotomus like nearly all octopuses, is semelparous (Van Heukelem 1979, Arnold and Williams-Arnold 1977, J.M. Arnold 1984, but see also Rodaniche

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Table 2.1. Octopodidae known to have capacity for arm autotomy.

Species	Type locality
Ameloctopus litoralis Norman, 1992	GBR*, Australia
Euaxoctopus panamensis Voss, 1971	Gulf of Panama
Euaxoctopus pillsburyae Voss, 1975	Southern Caribbean
Octopus alecto Berry, 1953	Gulf of California
Octopus defillipi Vérany, 1851	Mediterranean Sea
Octopus horridus group:	
Octopus abaculus Norman and Sweeney, 1997	Philippines
Octopus aculeatus d'Orbigny, 1826	Philippines
Octopus arborescens (Hoyle, 1904)	Ceylon (Sri Lanka)
Octopus argus Krauss, 1848	Natal Prov., South Africa
Octopus bandensis Hoyle, 1885	Banda, Indonesia
Octopus filamentosis Blainville, 1826	Mauritius
Octopus harmandi de Rochebrune, 1882	South Vietnam
Octopus horridus Audouin *in*: Audouin & Savigny, 1826	Red Sea
Octopus mutilans Taki, 1942	Japan
Octopus niveus Lesson, 1830	Bora Bora (Society Is.)
Octopus quangdongensis Dong, 1976	Quangdong Prov., China
Octopus tenebricus Smith, 1884	GBR, Australia
Octopus tonganus Hoyle, 1885	Tonga
Octopus sp. 1 Norman, 1993	[GBR, Australia]
Octopus sp. 2 Norman, 1993	[GBR, Australia]
Octopus sp. 2 Norman and Sweeney, 1997	[Philippines]

*Great Barrier Reef

Omitted are *Octopus aranea* d'Orbigny, 1835, junior synonym of *O. filamentosis* and *Octopus fimbriatus* Ruppell *in*: Férussac & d'Orbigny, 1840, junior synonym of *O. horridus* (Norman pers. comm.)

1984, and Villanueva 1992) with a short lifespan (Ward and Norman, in prep.). The hectocotylized right third arm (R3) of males delivers spermatophores to the oviducts of females. Depending on regeneration time, fitness of a male octopus would be greatly reduced if it autotomized the hectocotylized arm prior to mating. To test whether this spermatophore-delivery arm was preserved from autotomy, comparisons of autotomy frequency were made between the hectocotylized arm of males and other arms of males, and between the hectocotylized arm of males and the corresponding arm of females. Rates of arm regeneration in animals at different life stages were also measured.

Enlarged suckers on octopuses, found on arm pairs 2 and 3 of mature males in this species, have been proposed to play a role in visual mate recognition (Packard 1961) and as providing heightened chemoreceptivity of chemical cues released by receptive females (Voight 1991), although this latter role has been questioned (Norman, pers. comm.). The autotomy plane is located between suckers 4 and 7 on all arms, proximal to the enlarged suckers, which are typically suckers 8-12 (Fig. 2.1). If enlarged suckers raise male fitness by increasing mating success or by decreasing injury to males resulting from mistaking other males for receptive females (Lutz and Voight 1994, Voight 1991), then male octopuses should autotomize arms bearing enlarged suckers at lower frequencies than other arms. The autotomy frequency of arms bearing enlarged suckers were compared to those without enlarged suckers in males; comparisons were also made with the same arms in females.

Although arm autotomy has been reported in several octopus species, no studies have reported the frequency of autotomy in nature. I estimated the incidence of arm autotomy and arm breakage in nature by recording the occurrence of regenerating arms in this species from both causes in wild specimens, and by measuring the rate of regeneration of arms in captive animals.

Anatomical specializations for autotomy vary considerably among taxa, but may be classified into three categories: those that facilitate severance of the body part, those

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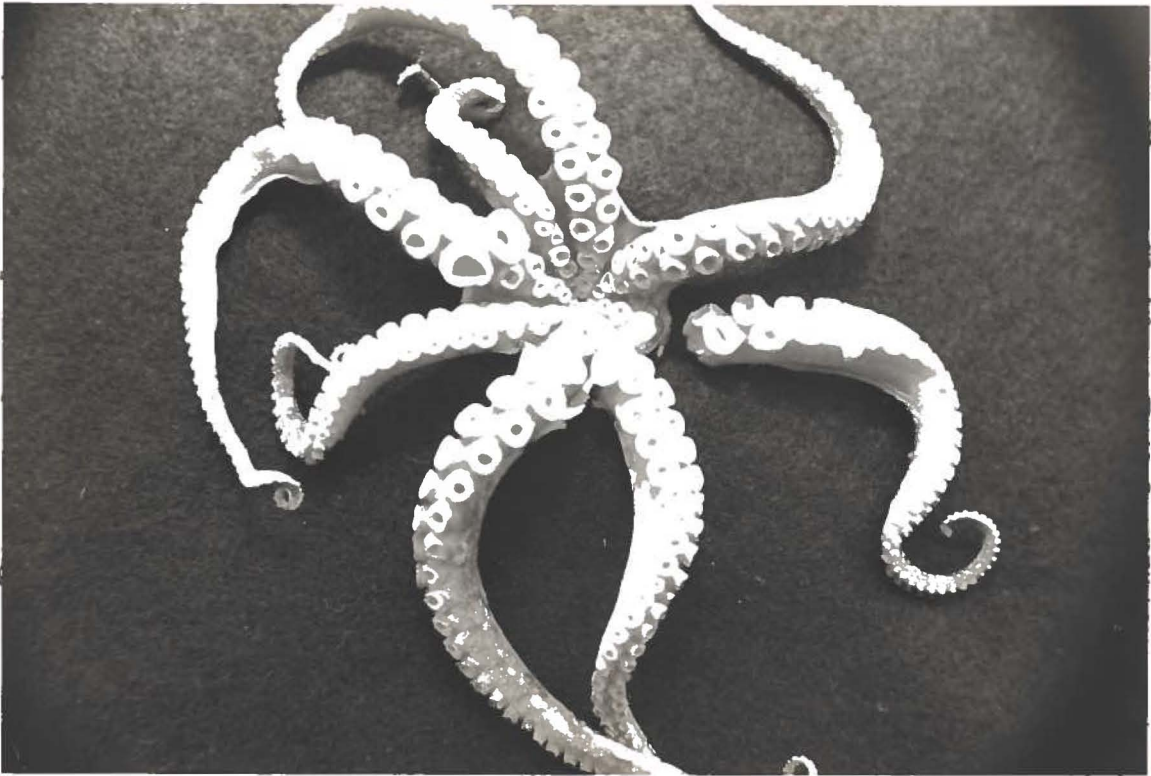
Figure 2.1. Arm autotomy plane is located between suckers 4 and 7, proximal to enlarged suckers on male arm pairs two and three.

that minimize the damage incurred, and those that facilitate subsequent regeneration (McVean 1975). Two types of autotomy planes have been described. The first is a permanent plane of least resistance (Wilkie 1978b), in which fracture occurs by the animal's own muscle action in combination with the resistance or pull of an opponent. The second is a potential plane of weakness (Wilkie 1978b), which is not demonstrable before autotomy but is modified by some rapid physiological process during autotomy to provide a breakage plane. The autotomy zone in the arms of *Octopus brachiotomus* was investigated using histological section in order to describe the breakage plane.

Materials and Methods

Arm loss in nature

Thirty-two female and 44 male octopuses were collected on intertidal to shallow subtidal reef flats on Guam between January 1993 and May 1995. Most collections were made during reef-walks during day and night low tides; a few animals were collected by snorkel or SCUBA during higher tides. Octopuses were captured by hand, using cotton gloves. As the octopuses autotomize arms only if the suckers attach to a surface, this method limited arm loss during collection, though some animals autotomized arms on to reef or container surfaces. Arms autotomized during capture were recorded and preserved. Arm loss existing at collection due to autotomy or breakage was also recorded.

Arm regeneration commencing between proximal suckers 4 and 8 was scored as autotomy; regeneration commencing at all other sites was attributed to breakage or other loss, which hereafter is termed breakage. Newly-autotomized arms, showing no tissue regeneration, were considered to have been lost during collection (whether or not the autotomy had been recorded), rather than classified as incidents of autotomy in nature.

As there is no scar on a fully regenerated arm, autotomy or breakage becomes increasingly difficult to identify as regeneration nears completion. Abrupt changes in sucker size (excluding enlarged suckers on males) and arm diameter were used as indicators of arm regeneration, especially when the arm in question was noticeably shorter than its opposing arm (excluding the 3rd arm pair in males). As arm tips are frequently missing, arm losses estimated at less than 10 mm length were not recorded as breakage.

The percent of arm length lost in a breakage event was estimated based on the opposing arm length minus length of the autotomy stub. The proportion of the arm lost was estimated for only those arms with a complete opposing arm.

<u>Autotomy tests</u>

Autotomy tests were performed on 12 females and 17 males. Animals were maintained separately in captivity for < 6 days before testing. After testing, animals were killed by anesthetizing in gradually cooled seawater for ≥ 3 h, rinsed in freshwater, fixed in 10% formalin for ≥ 2 weeks, then examined before preserving in 70% ethanol. No octopuses autotomized arms during anaesthetization or fixation.

Each autotomy test was performed by placing an octopus in a 30 x 40 cm white porcelain dish with ca. 3 cm seawater. I applied downward pressure with cotton-gloved fingers on an octopus arm chosen haphazardly. Duration in seconds was recorded until: a.) the octopus freed the trapped arm, b.) the octopus autotomized the arm, or c.) the arm broke. If none of these occurred, downward pressure on the arm was maintained for 120 s, after which time the arm was released. Trials were repeated on each octopus until three arms had been autotomized or broken, or for ten tests, whichever occurred first. In addition to haphazardly selected arms, the third right arm was tested on each octopus. If an octopus inked, seawater was changed between tests. Though tested octopuses often retreated to corners of the dish, they were prompted to move toward the center of the dish by a light touch on the side of the octopus facing the corner. Tests were not conducted until octopuses were in positions in the dish in which their movements were unobstructed.

<u>Regeneration</u>

Rates of arm regeneration were measured on six male and eight female octopuses that were kept in captivity for 11-63 days after autotomy. The lengths of regenerated portions of autotomized arms were measured on fixed animals. The length of the regenerated portion was multiplied by a ratio of mean octopus mantle length (26 mm, n=56) to the individual octopus' mantle length and divided by time elapsed, to give a regeneration rate adjusted for animal size. The condition of the octopus was noted as

Growing (sub-mature, eating well), Good (mature, eating well), Brooding (females having deposited eggs and no longer eating), or Senescing (males whose food intake had decreased by at least half their prior intake, or females who eventually died following cessation of eating, without depositing eggs).

Histological investigation

To investigate morphological adaptations for arm autotomy, the autotomy plane was examined histologically. Transverse, 10 μm sections of autotomized arms at the level of the severance plane, and portions of unautotomized arms between suckers 4 and 6 were prepared following Kier's (1992) methods, for both male and female specimens. Alternate slides of 8-12 sections were stained in Milligan trichrome and picro-ponceau with haematoxylin.

Results

Arm loss sites

The sites of natural and laboratory test arm losses from 23 females and 35 males were compiled in a frequency distribution (Fig. 2.2). Of 210 arm losses, 62% occurred following suckers 4-7, the autotomy site for this species.

Approximately 20% of *Octopus brachiotomus* were regenerating one or more arms due to autotomy in nature (Table 2.2). The figures are conservative, as very recent autotomies not yet showing tissue regeneration were not included in this calculation. Arms nearly or completely regenerated from autotomy or other arm loss leave no scar and could not be detected.

Autotomy in nature

Arm breakage occurred over twice as frequently as did arm autotomy in females, and nearly 3 times as frequently in males (Table 2.2). There were no significant differences between females and males in the proportions of individuals showing
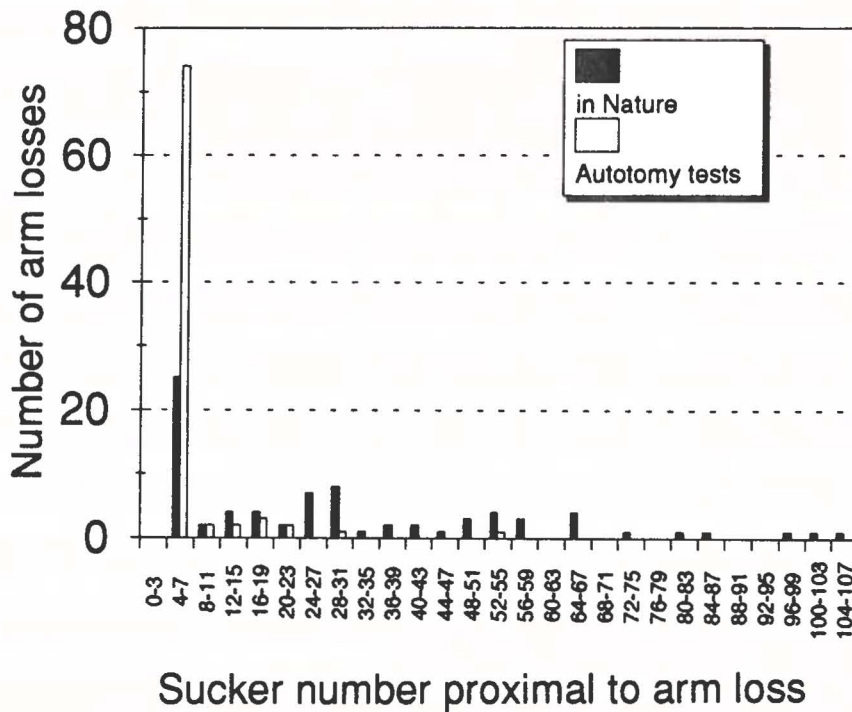
Figure 2.2. Frequency distribution of arm loss sites (n=58 animals)

Table 2.2. Frequency of arm loss in nature in *Octopus brachiotomus*.

	Females (n=24)		Males (n=37)	
Number of octopuses regenerating arm(s) lost by autotomy p > 0.05‡	5	(21%)	8	(22%)
Number of arms regenerating from autotomy p > 0.05‡	12	(6%)	13	(4%)
Number of octopuses regenerating arm(s) lost by breakage p > 0.05‡	11	(46%)	22	(60%)
Number of arms regenerating from breakage p > 0.05‡	18	(9%)	37	(13%)
% arm length lost in arm breakage p > 0.05§	62% SD 22%		52% SD 17%	

‡Female and male values compared with G-test of independence

§Female and male values compared with unplanned comparisons among pairs of means using the Games and Howell Method

autotomy or other arm loss. The difference in proportion of arms lost between males and females was not significantly different.

Autotomy tests

In 76 laboratory arm autotomy tests with 17 males, ranging in total length from 96 to 176 mm, the hectocotylized arm was never autotomized (Table 2.3), nor was autotomy of this arm ever encountered in males in nature. In two test cases arm R3 broke where downward pressure on the arm was applied: one at sucker 13, the other at sucker 20, indicating the arm would fail structurally before the octopus would release it through autotomy. Males characteristically hid the hectocotylized arm under other arms or under the mantle during tests, and often during routine handling. Males autotomized over half of the other arms tested.

Arm	Number of Tests	Arms Autotomized		Arms Broken	
L1	6	4	(67%)	0	(0%)
L2	13	8	(62%)	0	(0%)
L3	12	7	(58%)	1	(8%)
L4	5	2	(40%)	1	(20%)
R1	7	1	(14%)	2	(29%)
R2	6	2	(33%)	0	(0%)
R4	10	7	(70%)	1	(10%)
All arms except R3	59	31	(53%)	5	(8%)
R3	17	0	(0%)	2	(12%)
All arms	76	31	(41%)	7	(9%)

Table 2.3. Arm autotomy in male *Octopus brachiotomus* (n=17).

Autotomy of R3 vs. all other arms, G-test of independence: $p < 0.001$

Similar autotomy tests with 12 females showed no preservation of arm R3 from autotomy as compared with other arms (Table 2.4): 64% of R3 arms were autotomized versus a mean of 54% of all other arms. In two cases, as with males, arm R3 broke during tests: one at sucker 12, the other at sucker 22. The latter R3 arm, within 8 s of breaking, however, autotomized the distal 22 mm by "walking away" on its suckers from the body, although no external force was then applied. The autotomy process had

Table 2.4. Arm autotomy in female *Octopus brachiotomus* (n=12).

Arm	Number of Tests	Arms Autotomized		Arms Broken	
L1	4	2	(50%)	0	(0%)
L2	8	3	(38%)	0	(0%)
L3	6	4	(67%)	1	(17%)
L4	7	3	(43%)	1	(14%)
R1	3	2	(67%)	1	(33%)
R2	5	3	(60%)	0	(0%)
R4	2	2	(100%)	0	(0%)
Arms L1-R2 & R4	35	19	(54%)	3	(9%)
R3	11	7	(64%)	2	(18%)
All arms	46	26	(57%)	5	(11%)

Autotomy of R3 vs. all other arms, Fisher's exact test of independence: $p > 0.05$

apparently been triggered before the arm failed, and continued even though the stimulus was removed.

To test whether arms bearing enlarged suckers (L2, L3, R2, R3) on mature males were autotomized less readily than the other four arms, four tests were made (Table 2.5); all tests exclude the hectocotylized arm as it was never autotomized in tests nor in nature. The first test compared the incidence of autotomy in males in nature between arms L2, L3, R2 and arms L1, L4, R1, R4. The second test compared the incidence of autotomy between males and females of arms L2, L3, R2 in nature. The third test compared the incidence of autotomy in males in laboratory tests between arms L2, L3, R2 and arms L1, L4, R1, R4. The fourth test compared the incidence of autotomy between males and females in laboratory tests of arms L2, L3, R2.

None of the four tests show any preservation from autotomy of male arms bearing enlarged suckers, nor any significant difference in autotomy rate in corresponding arms of males and females (Table 2.5).

Among the octopuses tested for arm autotomy, four animals, all males, did not autotomize any arms tested. In some cases, the octopus pulled against the downward pressure applied on the arm; in other cases, no tension was evident in the tested arm.

Table 2.5. Autotomy of male arms bearing enlarged suckers vs. other arms, and vs. female arms.

Test Description	Total Arms	Arms Autotomized		Arms Broken	
1. Males in nature, n=37					
a. Arms L2, L3, R2	111	5	(5%)	17	(15%)
b. Arms L1, L4, R1, R4	148	8	(5%)	17	(12%)
a vs. b arms autotomized, G-test of independence: p > 0.05					
2. Females in nature, n=24					
c. Arms L2, L3, R2	72	4	(6%)	5	(7%)
d. Arms L1, L4, R1, R4	96	6	(6%)	9	(9%)
a vs. c arms autotomized, Fisher's exact test of independence: p > 0.05					
3. Males, autotomy tests, n=17 animals					
e. Arms L2, L3, R2	31	17	(55%)	1	(3%)
f. Arms L1, L4, R1, R4	28	14	(50%)	4	(14%)
e vs. f arms autotomized, G-test of independence: p > 0.05					
4. Females, autotomy tests, n=12 animals					
g. Arms L2, L3, R2	19	11	(58%)	1	(5%)
h. Arms L1, L4, R1, R4	16	9	(56%)	2	(13%)
e vs. g arms autotomized, G-test of independence: p > 0.05					
g vs. h arms autotomized, G-test of independence: p > 0.05					

Of these four animals, however, one autotomized an arm at capture, and in a second test 60 days after the first, the same octopus autotomized three arms tested. The second animal autotomized an arm during routine handling 71 days after testing. The third animal, tested a second time after 83 days, autotomized two arms tested. The fourth octopus died in captivity before a second test was conducted. Generally, the longer animals were kept, the less readily they autotomized arms in normal handling (except for brooding females). It was therefore unexpected that these males autotomized arms more readily after relatively long periods of captivity than before. The fact that three of these four animals autotomized arms at other than test times indicates that temporal variation in willingness to autotomize may be greater than variation among individuals in willingness to autotomize. This variation is consistent with behavioral control of the autotomy process.

Although no autotomy of a male hectocotylized arm was seen in nature or in tests, loss of this arm to breakage does occur in nature. Three males were regenerating arm R3 (at suckers 18, 31 and 32) from non-autotomy losses when captured. Loss of the arm also occurred immediately prior to death in some captive males. When maintained in captivity through senescence and death, many males and females apparently bit off portions of one or more arms (autophagy) in the final hours of life. The frequency of autophagy of the hectocotylized arm of males was not significantly less than the mean frequency of autophagy in other arms (Table 2.6). Of the 12 males kept through senescence, two males did remove their hectocotylized arms, at suckers 8 and 19. One excised hectocotylized arm could not be found and may have been ingested; the other arm remained in the container with the octopus. A third senescing male apparently did autotomize arm R3 at sucker 5, though no trace was found of the arm. The proximal end of the arm was cleanly severed, rather than ragged and torn as were arms removed by autophagy. In addition, despite the well-known extensibility of octopus arms, it seems quite improbable that this male could have bitten off its own arm only 11 mm from its mouth; other cases of autophagy left arm stubs 18-82 mm in length, and three other

Table 2.6. Arm autophagy in senescing octopuses in the laboratory.

Arm	Females (n=11) Autophagy		Males (n=12) Autophagy	
L1	2	(18%)	2	(17%)
L2	3	(27%)	4	(33%)
L3	1	(9%)	2	(17%)
L4	2	(18%)	6	(50%)
R1	1	(9%)	3	(25%)
R2	1	(9%)	3	(25%)
R4	2	(18%)	1	(8%)
Arms L1-R2 & R4	12	(16%)	21	(25%)
R3	2	(18%)	2	(17%)
All arms	14	(16%)	23	(24%)

Male autophagy of R3 vs. all other arms, Fisher's exact test of independence: $p > 0.05$
Female vs. male autophagy, all arms, Fisher's exact test of independence: $p > 0.05$

arms of this same octopus were torn off distally much further, at 57 mm, 71 mm, and 72 mm. This incident indicates that an autotomy mechanism exists in the hectocotylized arm as in all other arms.

Regeneration

Size-adjusted regeneration rates of autotomized arms ranged from 0 - 9.9 mm/week (Table 2.7); in some cases the rate difference among arms regenerating on the same octopus during the same time period was considerable. Of two mature, apparently healthy males kept in captivity, fed *ad libitum* for twelve days following autotomy tests, one male (M2) regenerated 5 mm and 2 mm on two left arms, while no regeneration was evident on the right arm; nor was any regeneration seen on any of the three autotomized arms of the other male (M1) who was concurrently regenerating arm R3 from a non-autotomy loss.

Females of this species characteristically cease eating 0-3 days prior to egg deposition, brood their eggs for the 20-day development period, and die within 10 days of egg hatching. Arms autotomized by females during egg-laying typically regenerated at low rates. Two females (F3, F8) regenerated arms lost before they deposited eggs at size-adjusted rates of 3.1, 3.0 and 3.5 mm/week. However Female 3 regenerated arm L4 lost during egg laying at only 1.4 mm/week.

Male senescence usually lasts somewhat longer than that of females, as males decrease food intake gradually rather than abruptly. By late senescence, however, much body tissue has been converted to energy for metabolic functions. Arms autotomized during senescence by males, and by females in the latter stages of brooding, typically regenerate at even lower rates. Female 4 (F4) and male 5 (M5) regenerated arms at size-adjusted rates of 0.7, and 0.4 mm/week even though less than half the regeneration occurred during senescence.

Table 2.7. Regeneration rates of autotomized arms, adjusted for animal size.

Sex, No.	Mantle length mm	Arm	Concurrently regenerating autotomies	breaks	Days regenerated	Gr	Gd	Br	Se	Regenerated arm length (mm)	Size-adjusted regeneration rate (mm/wk)
F1	~10[1]	R1	0	0	60	100				~16	4.9*
F2	20	R4	0	0	61		67	33		42	6.3
F3	24	R4	0.28[2]	0	39		69	31		16	3.1
		L4	1	0	11			100		2	1.4
F4	25	L3	0	?[3]	34		56		44[3]	3	0.7
F5	26	L4	0	?[4]	49		53	47		41	5.9
F6	27	R4	0	0	28			100		0	0.0
F7	28	R1	1	0	63		79	21		29	3.0
		L1	1	0	63		79	21		25	2.6
F8	32	L2	1	?[5]	44		43	57		23	3.0
		R2	1	?[5]	44		43	57		27	3.5
M1	22	L1[6]	2[7]	0	12	100				0	0.0
		L2[6]	2[7]	0	12	100				0	0.0
		L3[6]	2[7]	0	12	100				0	0.0
M2	25	L2[6]	4	1	12	100				5	3.0
		L3[6]	4	1	12	100				2	2.4
		R4[6]	4	1	12	100				0	0.0
M3[8]	26	R4	0	4	67	100				60	6.3*
M4	28	R2	0	2	38	100				58	9.9*
M5	29	L2	1	2	44		59		41	3	0.4
M6	30	R4	0.75[2]	3	56	100				64	6.9
		R2	1	3	42	100				49	7.1

[§]Conditions: Gr: Growing; Gd: Good, eating well; Br: Brooding; Se: Senescing

*3 octopuses in good condition regenerating only 1 arm from autotomy used to calculate mean time to complete arm regeneration

[1]Mantle length and arm regeneration length estimated from the live octopus
[2]Fractional value indicates an arm was autotomized later in the regeneration period
[3]Unclear, autophagy of 4 arms; this female did not deposit eggs in 42 days of captivity
[4]Unclear, autophagy of 4 arms 10 days after her eggs hatched
[5]Unclear, autophagy of 3 arms 5 days after her eggs hatched
[6]Experimental arm autotomy; all others occurred during capture or routine handling
[7]Male was also regenerating arm R3 from a pre-existing breakage
[8]Octopus was missing second gill

Regeneration rates typical of males and females that are eating, in good condition, and regenerating only one autotomized arm are seen in F1, M3, and M4. Complete arm regeneration times were observed as 60 days for F1, and estimated, based on proportion

of original whole arm length attained during regeneration period, as 61 days for M3, and 80 days for M4. The mean of these values and an estimate of arm regeneration time for *Octopus brachiotomus* in good condition is 67 days (SD=11).

<u>Histological investigation</u>

No plane of weakness or unusual structure recognizable with histology staining techniques typically applied to cephalopod arms (Kier 1992) was found on 10 μm sections using light microscopy.

Discussion

<u>Autotomy in nature</u>

Arm autotomy is not liberally employed by *Octopus brachiotomus* in nature in Guam. Regeneration of one or more arms lost by autotomy was evident in 21% of females and in 22% of males. Based on a 7-month lifetime (Ward and Norman in prep.) and complete arm-regeneration time of 67 days, the probability of an octopus of this species that lives to reproductive age autotomizing at least one arm in its lifetime is 0.7 (Table 2.8). Individual octopuses may, however, be regenerating more than one arm concurrently from autotomy.

Arm regeneration from breakage was evident in over twice the number of octopuses regenerating arms from autotomy: 46% of females and 60% of males. Considerably less arm tissue is characteristically lost in an arm break or predator bite than in autotomy, requiring less time and energy to complete regeneration. Based on

Table 2.8. Estimates of lifetime arm loss from autotomy and breakage for *Octopus brachiotomus*.

	Females	Males
Lifetime arm autotomy	0.7	0.7
Lifetime arm breakage	2.3	3.6
Lifetime total arm loss	3.0	4.3

1.) 7-month octopus lifetimes, 2.) 62% arm length loss in the mean female arm break and 52% arm length loss in the mean male arm break (Table 2.2), and 3.) rate of arm regeneration the same as with autotomy, an average female can be estimated to suffer at least one arm breakage 2.3 times, an average male 3.6 times during their lives.

There are several implications of these estimates of arm loss rates. First, the octopuses live high-risk existences: average females suffer 3, average males over 4, partial or complete arm losses during their short lifetimes. Second, octopuses presumably control the occurrence of autotomy, choosing to employ it as a defense strategy in only 1/6 to 1/4 of arm breakage incidents. Third, autotomy in this animal is apparently not a reflex action.

Autotomy tests

No autotomy of a male hectocotylized arm was found in nature or in autotomy tests due, evidently, to its overriding significance as the organ of spermatophore delivery. There is evidence from one senescent male which apparently autotomized arm R3 a few hours before death, that the arm is functionally capable of autotomy, and that the barrier to its loss is most likely behavioral rather than physiological.

Although an adult *Octopus brachiotomus* can regenerate arms lost via autotomy in approximately 10 weeks, that period constitutes a considerable proportion of its estimated 7-month life span. If an adult male autotomized the spermatophore delivery arm, his opportunities for successful mating would most likely be significantly reduced, in the worst case resulting in a fitness of zero.

Histological investigation

No plane of weakness or unusual structure was evident in histological investigation of the autotomy area of autotomized or of unautotomized arms. Lack of visually apparent (with light microscopy) histological specializations for arm autotomy have been noted in other organisms which undergo autotomy. Bickell-Page (1989) found that

enervated granule-filled cells degranulate during autotomy in the nudibranch *Melibe leonina*; these granules were not resolvable in even 1 μm sections, although a granular zone at the base of the deciduous cerata of three species of the nudibranch genus *Doto* was identified using light microscopy (Kress 1968 in Bickell-Page 1989). Bickell-Page and Mackie (1991) also found that examination of tentacle sections of hydromedusa *Aglantha digitale* after autotomy revealed little about the mechanism. Wilkie and Emson (1987) used electron microscopy to find the granule-containing juxtaligamental cell processes associated with sites of potential autotomy in an ophiuroid. Norman (1993a), however, identified a "weak point in the longitudinal muscle with higher densities of nuclei on either side of the autotomy plane in each of the eight arms" of *Ameloctopus litoralis* with histological sections and light microscopy. Norman (personal communication) has examined the autotomy zone in *Octopus brachiotomus* specimens but has not found a similar structural weakness. Norman's (1993a) cladistic analysis of the Octopodinae of the Great Barrier Reef suggests that arm autotomy evolved independently in *Ameloctopus litoralis* and in the *Octopus horridus* group, in which *Octopus brachiotomus* belongs (Ward and Norman in prep.) Thus the mechanisms of autotomy in the two groups may be different, as suggested by these histological investigations.

Regeneration

Excellent regenerative capacity is characteristic of cephalopods (Lange 1929, Nesis 1987 p. 84), and its prevalence in the group indicates it to be a more primitive trait than arm autotomy. The pre-existence of regenerative powers may have facilitated the multiple evolution of autotomy in this group.

Evolutionary implications of autotomy

Tail autotomy in lizards is useful in two ways (E.N. Arnold 1984): it allows an animal held by the tail to escape its predator's grasp, and the actively twitching tail

provides a distraction away from the lizard's vulnerable head and body, allowing it more time to escape. In snakes and lizards (Squamata), intravertebral tail autotomy and regeneration is apparently primitive, though it has been lost in several groups, or lost and recovered in a simpler, intervertebral form (E.N. Arnold 1984). Those in which autotomy has been lost fall into three main groups: very large lizards that can actively defend themselves or that live on islands where predation levels are low; slow lizards, smaller in size, with modest-size tails; and lizards whose primary habitat is complex vegetation, where escape by speed is difficult, either because the animal is slow, or because it is hampered by the terrain.

The benefits of autotomy are likely to be low, Arnold proposes, if: predation is rare; the animal can protect itself effectively in other ways (e.g. it is large); escape is difficult either because the animal is slow or because it is hampered by the terrain; or the portion of tail autotomized is too small or unappealing to distract the predator. Conversely, autotomy is likely to be more beneficial to small species, and use of the autotomized organ to divert attack from the head and body more important for "delicately constructed forms" (p. 138) with limited ability to fight back compared with more robust species. Likewise, Pakarinen (1994) proposes that autotomy evolved more frequently in terrestrial slug species which rely on escape into hiding, than in those slug species whose physiology or environment do not enable them to hide quickly after an attack.

Octopus brachiotomus is a small animal living in a high-risk environment with few defenses against predators; it can escape quickly into reef crevices and if necessary, autotomize a writhing arm of sufficient size to interest many predators. Compared to several other octopuses sharing its shallow water habitat on Guam, this species is small (total length averages 145 mm, weight averages 13 g). Sympatric *O. cyanea* reach weights of several kg (Norman 1991), while *O. ornatus* reach weights of at least 1 kg (Norman 1993b). Although many *O. cyanea* encountered are regenerating at least one

arm break (personal observation), an adult of that species is a large animal that, at least as reported in Hawaii, few reef predators can subdue (Van Heukelem 1966). Although co-occurring *O. ornatus* do not reach the large body size of *O. cyanea*, they are considerably larger than *Octopus brachiotomus*, and limit their activity to night when larger visual predators may be less successful. Because of its considerably smaller size, *Octopus brachiotomus* may be the potential prey of more predator species than are its larger congeners.

Autotomy in benthic octopuses appears to occur in those species which have long arms relative to mantle length (Norman 1993a) (arm mantle index, AMI > 300) and which are neither pygmy nor massive (15 g ≤ adult weight < 100 g) (Table 2.9). *Octopus brachiotomus* falls within these parameters. Of the 32 Great Barrier Reef, Philippine, and Guam species in Table 2.9, only three exceptions to this pattern occur: *Octopus* sp. 1 Norman & Sweeney, 1997; *O. nocturnus*; and *O. aculeatus*. A binomial test comparing the species predicted to have arm autotomy, based on arm length and weight, versus those that fall outside the prediction, indicates that together, arm mantle index and weight significantly predict arm autotomy (no weight is available for *Octopus tenebricus* which is excluded from the binomial test). Consistent with Arnold's work, octopus species of greater mass may be able to defend themselves more effectively and may be less able to hide quickly, while a detached arm of a pygmy or short-arm species may not effectively distract predators from the octopus' body.

Defense mechanisms available to *Octopus brachiotomus*, aside from autotomy, are limited to flight by jetting or crawling, inking, combat using sucker- attachment on the predator, and biting. Unlike arm autotomizing *Ameloctopus litoralis*, which keeps its body hidden under rocks or in the reef lattice as its arms search for prey, and no longer has a functional ink sac (Norman 1992), *Octopus brachiotomus* retains its ink sac. Its ink is an effective visual distraction, but it is displaced, though not dispersed, quickly in flowing water. There are no records of this animal's bite, but considering its small beak

Table 2.9. Weight and arm mantle index (AMI) of octopuses in relation to the capacity for arm autotomy. Based on all octopus species recorded from the Great Barrier Reef by Norman (1993a) and from the Philippines by Norman and Sweeney (1997). *Octopus brachiotomus* included for comparison.

Species	Maximum weight, g	Maximum mantle length, mm	Arm : mantle AMI	Weight ≥ 15 g < 100 g	AMI > 300	Arm autotomy
Hapalochlaena lunulata (Quoy & Gaimard, 1832)	2	31	200	-	-	no
Octopus sp. 3 Norman & Sweeney, 1997	6	21	250-350	-	-	no
Octopus bocki Adam, 1941a	9	25	250-400	-	+	no
Octopus wolfi Wülker, 1913	12	15	150-200	-	-	no
Octopus sp. 5 Norman & Sweeney, 1997	12	24	300-450	-	+	no
Octopus pumilus Norman & Sweeney, 1997	12	31	250-300	-	-	no
Ameloctopus litoralis Norman, 1992	15	40	540-1000	+	+	yes
Hapalochlaena sp. 1 Norman 1993a	15	38	180-220	+	-	no
Octopus polyzenia Gray, 1849	19	38	215-290	+	-	no
Octopus abaculus Norman & Sweeney, 1997	21	33	450-600	+	+	yes
Octopus brachiotomus	28	33	300-715	+	+	yes
Octopus sp. 1 Norman & Sweeney, 1997	32	45	320	+	+	no
Octopus sp. 2 Norman & Sweeney, 1997	35	30	430-470	+	+	yes
Octopus sp. 2 Norman, 1993	60	42	400-500	+	+	yes
Octopus aegina Gray, 1849	60	62	200-300	+	-	no
Octopus nocturnus Norman & Sweeney, 1997	62	60	400-750	+	+	no
Octopus sp. 1 Norman, 1993	75	60	490-670	+	+	yes
Octopus exannulatus Norman, 1993b	75	50	200-310	+	-	no
Macroctopus aspilosomatis (Norman, 1992b)	120	87	438-640	-	+	no
Octopus cf. *vitiensis* Hoyle, 1885	121	42	400-500	-	+	no
Octopus aculeatus d'Orbigny, 1835	121	63	500-600	-	+	yes
Octopus sp. 4 Norman & Sweeney, 1997	123	42	400-500	-	+	no
Octopus sp. 3 Norman, 1993	130	75	200-280	-	-	no
Octopus marginalis Taki, 1964	175	80	200-280	-	-	no
Octopus mototi Norman, 1992a	300	100	250-310	-	-	no
Octopus cf. *luteus* Sasaki, 1929	320	90	400-550	-	+	no
Macroctopus alphaeus (Norman, 1992b)	340	80	316-508	-	+	no
Cistopus indicus (Rapp, 1835, in Ferussac & d'Orbigny, 1834-1848)	357	86	200	-	-	no
Octopus ornatus Gould, 1852	1000	130	550-800	-	+	no
Macroctopus dierythraeus (Norman, 1992b)	1500	135	366-574	-	+	no
Macroctopus graptus (Norman, 1992b)	4200	191	447-707	-	+	no
Octopus cyanea Gray, 1849	6000	160	400-600	-	+	no
Octopus tenebricus Smith, 1884	n/a	19	320-380	?	+	yes?

Using binomial test, p < 0.0014 that octopus species weighing ≥ 15 g but < 100 g with arm : mantle index > 300 are by chance the species with the capacity for arm autotomy (excludes *O. tenebricus*).

size (rostrum 2-3 mm) and the necessary exposure of its vulnerable head and mantle to gain biting position, biting is probably of limited defensive use.

Like other octopuses, *Octopus brachiotomus* moves moderately quickly, not with the remarkable burst of speed of many small reef fishes, but reasonably quickly by jetting in the water column, often releasing a small ink cloud, or by crawling and rapidly squeezing its highly compressible body into tiny crevices in the structured reef.

A typical autotomized adult arm is 70-90 mm long, weighing 0.8 - 2.4 g, a reasonable catch for many predators. The detached arm is immediately active, especially so when in contact with an organic surface such as a hand. In these respects *Octopus brachiotomus* shares characteristics with autotomizing lizards and snails: it is relatively small, but can escape quickly; it faces at least moderate predation pressure with few defenses; the autotomized organ is active and of sufficient size to interest many predators.

Autotomy may serve *Octopus brachiotomus* in the same two ways proposed (E.N. Arnold 1984) for lizards: to achieve release from a predator's grasp, and to draw the predator's attention to a writhing arm which may attach to the attacker, away from the vulnerable head and mantle, providing opportunity for the octopus to escape.

Compared with other animal groups, there is still very little known of autotomy in octopuses. This study provides preliminary insights into this distinctive defensive behavior, relatively rare in the over 200 species of octopuses described to date. Further studies could examine the autotomy zone with electron microscopy, and compare autotomy frequency in this species with other shallow water octopuses.

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