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Eggs and Larvae of *Graneledone* sp. (Mollusca, Octopoda) from New Zealand

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Abstract Two sets of eggs and larvae of species of bathyal octopus are described from New Zealand. Both sets of eggs are deposited in clusters, each cluster comprising large egg capsules with short stalks individually cemented to the substratum. Egg capsules from both clusters are similarly teardrop-shaped and without apparent external sculpture, however, capsule and stalk lengths differ between the two, 24.0–26.2 × 1.5–3.0 mm and 20.5–21.7 mm × 2.0–3.6, respectively. Larvae just hatching out the capsules from one set of eggs are attributed to the genus *Graneledone*, while the second set of eggs without larvae cannot presently be identified to the generic level. A comparison between larval, juvenile and adult stages of *Thaumeledone* and *Graneledone* species is made.

Keywords Mollusca, Octopoda, *Graneledone*, larvae, eggs, New Zealand.

Introduction

There has been little systematic research on the bathyal and abyssal octopod fauna of New Zealand subsequent to the description of several species over a century ago in the Challenger Report (HOYLE, 1886). Extensive collections of bathyal and abyssal octopus taxa have been developed over the last decade, concurrent with increased exploratory and commercial fisheries within New Zealand waters, that enable the deep-water octopus fauna of New Zealand to be comprehensively re-evaluated.

Four species of octopus have been described from New Zealand bathyal and abyssal depths: *Grimpoteuthis meangensis* (HOYLE, 1885), *Graneledone challengeri* (BERRY, 1914), *Graneledone* sp. KUBODERA, 1990 (as *Pareledone* sp.) and *Benthoctopus* sp. KUBODERA, 1990 (as *Octopus* sp.). Four sets of eggs also have been described: three clusters of 'Type B' eggs without apparent embryos

(ROBSON, 1932: 166, Plate 1, fig. 3), and two solitary eggs containing cirrate embryos (BOLETZKY, 1982). Where as incirrate eggs are attached to the substrate by chorion stalks, cirrate eggs are not (*fide* BOLETZKY, 1982). Although ROBSON (*loc. cit.*) was uncertain over the systematic position of his 'Type B' eggs, referring them to one of either incirrate or cirrate eggs, they are now recognised as typical of incirrate octopus species.

Two new clusters of eggs similar to ROBSON's 'Type B' eggs herein are described from New Zealand waters, one of which contains fully developed larvae. The larvae lack an ink sac and the suckers are arranged in a single row, a character combination common to three genera, *Graneledone*, *Thaumeledone* and *Bentheledone* (*fide* VOSS, 1988a). The most recent synopsis of eggs and larval stages in these rare bathyal and abyssal taxa cites for one species of *Graneledone* spawned egg capsule lengths of 35.0 mm and for *Bentheledone rotunda*, mature ovarian eggs of 16 mm length (HOCHBERG *et al.*, 1992). Mature ovarian egg dimensions for *Graneledone pacifica* VOSS and PEARCY, are given as 16×7 mm (VOSS & PEARCY, 1990). Neither mature ovarian eggs or egg capsules of species of *Thaumeledone* presently are described, however, a review of existing species currently is in preparation (HOCHBERG, pers. com.).

The description of egg capsules and larvae of bathyal and abyssal incirrate octopus species from New Zealand therefore adds to our knowledge of the biology of these deep-sea octopods.

Methods

The two sets of eggs and larvae of bathyal and abyssal octopus described herein have been divided between two repositories, the National Museum of New Zealand (NMNZ), Wellington, New Zealand, and the National Science Museum, Tokyo, Japan (NSMT). Material from the National Museum of New Zealand, the National Institute of Water and Atmospheric Research, Wellington, New Zealand (NIWA; collection acronym NZOI), the National Science Museum, Tokyo, the British Museum of Natural History, London (BMNH), the National Research Institute of Far Seas Fisheries, Shimizu, Japan (FSFRL), has been loaned or examined in the course of this research. Type material of *Graneledone challengeri* (BERRY, 1914), *Thaumeledone brevis* (HOYLE, 1885) and *T. gunteri* ROBSON, have been examined.

Anatomical characters in the larvae were assessed utilizing combinations of conventional dissection, light microscopy and scanning electorom microscope (SEM). Clearing and staining techniques for larval and juvenile fishes proposed by POTTHOFF (1984) were employed for observation of mantle tissue. All anatomical line drawings were prepared with the assistance of a camera lucida.

Standard morphometric indices, measurements and counts used in octopod

descriptions (see ROPER & VOSS, 1983), with the exception of ASC, here enumerated as whole arm sucker counts instead of half arm sucker counts. All descriptions and measurements are calculated from preserved specimens. All available larvae are to varying degrees distorted, making precise measurements difficult. Characters and measurements described for these larvae are limited to those that can accurately be enumerated or measured. As a consequence only a limited subset of characters proposed basic to octopus descriptions (ROPER & VOSS, *loc. cit.*) are presented.

Eggs and larvae examined

NMNZ M.119218, eggs, *ca* 37°05′S, 166°30′E, *ca* 1755 m, C.S.S. *Recorder*, col. W. Foster, 1932 (NW end of Challenger Plateau); NMNZ M.119219, *Graneledone* eggs + larvae, 44°37.30′S, 173°31.6′E, 784 m, 23/9/89, f.v. *Oyang 76*; NSMT-Mo68176, 2 egg capsules + 2 larvae selected from NMNZ M.119219, 44° 37.30′S, 173°31.6′E, 784 m, 23/9/89, f.v. *Oyang 76.*

Select additional material examined

NMNZ M.118324, *Graneledone challengeri* (BERRY, 1914), male, ML 89.5 mm, 39°59′S, 178°13′E, 940–1070 m, -/04/1994, f.v. *Peterson*; NZOI Stn S153, *Graneledone challengeri* (BERRY), female, ML 26.8 mm, 45°21.1′S, 173°35.8′E, 1386 metres, 27/10/79; NMNZ M.117874, *Graneledone* sp. (=*Pareledone* sp. KUBODERA, 1990), female, ML 147.0 mm, 48°27.30′S, 179°27.56′E, 565–599 m, 15/11/93; FSFRL EI219 (14-2-3), *Benthoctopus* sp. (=*Octopus* sp. KUBODERA, 1990), female, ML 120.5 mm, 48°58′S, 171°01.5′E, 644 m, 24/01/1976, f.v. *Shinkai Maru*; FSFRL EI259, *Graneledone* sp. (=*Pareledone* sp. KUBODERA, 1990), female, ML 69.0 mm, 48°15.5′S, 179°48.5′E, 512 m, 17/11/1975, f.v. *Shinkai Maru*; NZOI Stn S202, *Thaumeledone* sp., 3 males, ML 43.5, 42.0, 13.0 mm, 42°14.7–16.6′S, 175°08.6–10.6′E, 2476–2542 m, 02/11/1979; BMNH 1889.4.24. 50–51, *Thaumeledone brevis* (HOYLE, 1885), Syntypes, 2 females, ML 17.0, 8.1 mm, 37°17′S, 53°52′W, ca 1096 m, 14/02/1876 (*Challenger* Stn 320, off Monte Video); BMNH 1951.4.26.50, *Thaumeledone gunteri* ROBSON, 1930, Holotype, female, ML 37.7 mm, 53°48.30′S, 35°57′W, 21/01/1927, *ca* 409–400 m (*Discovery* Stn 158, N.E. of South Georgia).

Results

Distribution

The distribution of examined New Zealand egg, larval, comparative juvenile and adult material is depicted in Fig. 1. One set of eggs was collected from the Challenger Plateau near Lord Howe Rise (ROBSON, 'Type B' eggs; NMNZ M.119218) and the other one set was from the Chatham Rise (NMNZ

M.119219).

Description of eggs

The eggs are deposited in clusters, the number of eggs in each cluster is unknown due to total cluster fragmentation. One cluster contains 32 eggs

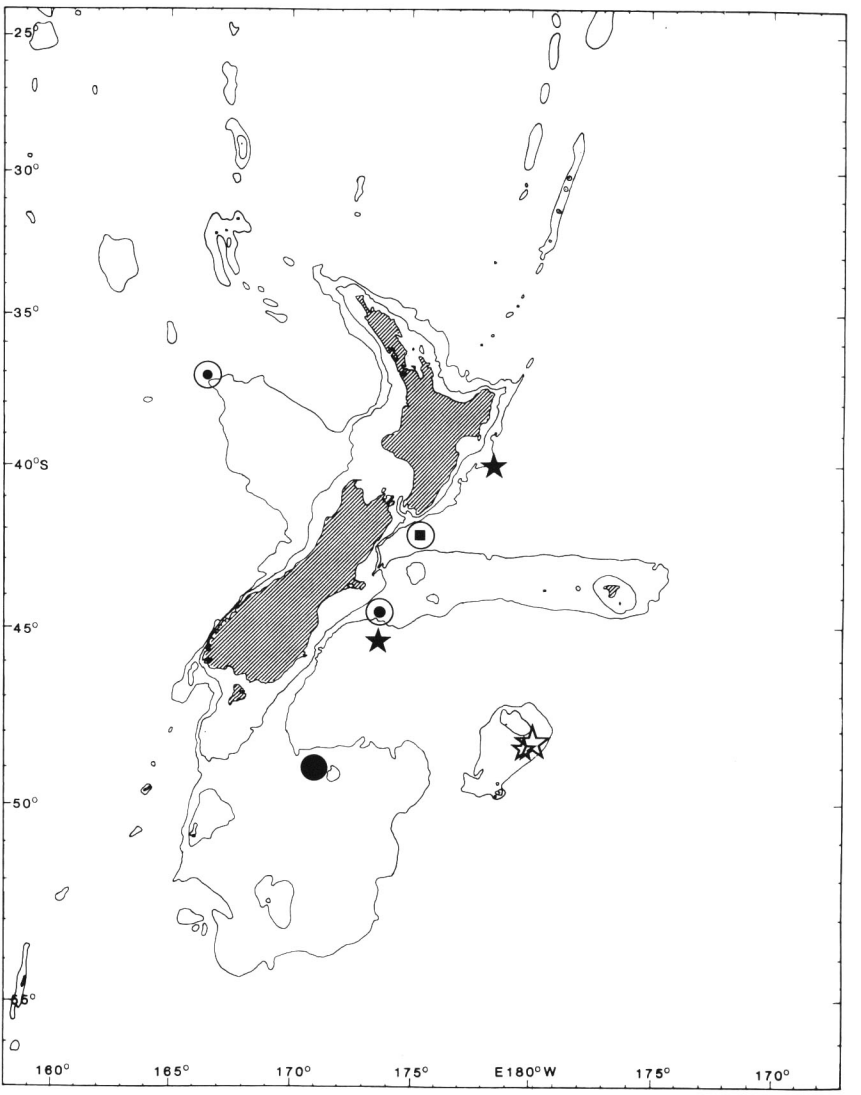

Fig. 1. Distribution of eggs, larvae, juveniles and adult specimens from New Zealand. ⊙: eggs, ★: *Graneledone challengerii*, ☆: *Graneledone* sp., ●: *Benthoctopus* sp., ◉: *Thaumeledone* sp.

(NMNZ M.119218), the other 23 eggs (NMNZ M.119219). Each egg is individually cemented to the substratum by a short stalk. The egg capsules in both clusters are similar in gross facies in that they are both tear-drop-shaped and lack apparent surface sculpture. Capsule and stalk lengths differ, 20.5–21.7 mm × 2.0–3.6 mm and 24.0–26.2 mm × 1.5–3.0 mm respectively (Table 1). All larvae in cluster NMNZ M.119219 protrude through fissures at the very base of the egg capsule near the short chorion stalk. The egg capsule of NSMT-Mo68176 is shown in Fig. 2(A, B). In some egg capsules a small amount of yolk remains despite the larvae appearing fully formed or breaking through the egg capsule. The second set of egg capsules, NMNZ M.119218, contain no apparent larvae and are evidently full of yolk.

Description of larvae

The least distorted larva available is figured in Fig. 2 (C=ventral, D=doral). Mantle length (ML) in the larvae ranges 9–13 mm. The mantle appears broad, mantle width ranging 90–116% ML, and is marked from the head by a weak constriction. The head similarly is broad, 80–111% ML, equal to or exceeding mantle width, and large, head length 38–55% ML. The head similarly is marked from the brachial crown by a weak constriction. Eye diameter is equivalent to head length, the head basically comprising two massive orbits meeting along the dorsal mid-line. The arms are short, 59.5% TL, 169% ML and well developed suckers, numbering 32 to 45, are distributed in a uniserial fashion along the entire arm length. Because of distorsion, neither arm or web formulas can be calculated for any specimen. The web does, however, appear to be well developed. Clusters of cartilaginous elements are not apparent in any specimen, however, the dorsal surfaces of mantle and head in some larvae are beset with

Table 1. Measures of seven individual eggs from each of two egg clusters.

octopod eggs *gen., sp. indet* dimensions (mm) NMNZ M.119218							
	1	2	3	4	5	6	7
Egg Length	21.0	20.5	20.5	21.2	21.2	21.7	21.0
Stalk Length	3.0	2.0	2.7	2.8	2.1	3.6	3.0
Egg Width	10.2	11.0	11.0	11.1	10.5	10.9	11.0
Graneledone egg dimensions (mm) NMNZ M.119219							
	1	2	3	4	5	6	7
Egg Length	24.5	24.5	26.2	24.0	24.9	25.0	24.6
Stalk Length	2.9	1.5	2.2	3.0	2.2	2.0	1.9
Egg Width	12.8	13.8	12.9	12.0	12.4	12.5	14.0

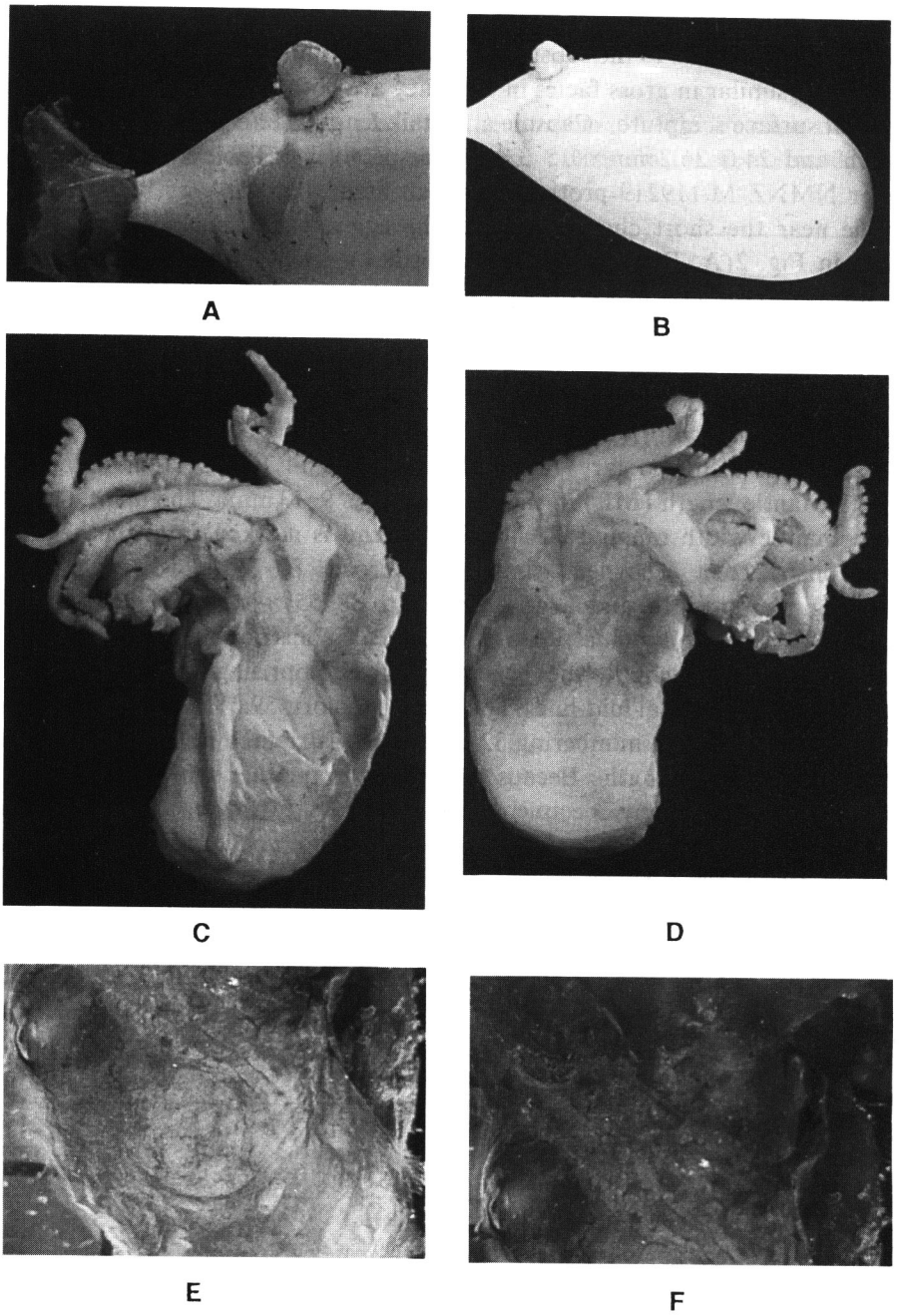

Fig. 2. Egg and larva of *Graneledone* sp. (NSMT-Mo68176) A: base portion of the egg and the substratum, B: egg capsule; C: ventral view of larva, D: dorsal view of larva, E–F: stained mantle skin.

large processes of a non-cartilaginous nature as determined from mantle tissue staining (Fig. 2: E, F).

Small red chromatophores, sparsely scattered over the dorsal surfaces of mantle, head, arms and web of the larvae, are more densely scattered over the ventral surfaces of same. The general colouration of the mantle, head and arms is otherwise a somewhat drab-pink-grey. The distribution of surface chromatophores indicates that the ventral surfaces of these structures are darker than the dorsal.

Mantle cavity

The gills are large and comprise 7 inner and outer lamellae per demibranch. Both demibranchs are well developed, the inner without apparent reduction. The interpallial septum is well developed and extends to the posterior end of the

Table 2. Measurments and counts of *Graneledone* and *Thaumeledone* species, standardised by ROPER and VOSS (1983).

	T. brev (S) BMNH	T. brev (S) BMNH	T. gunt (T) BMNH	Thaum sp. N S202	Thaum sp. N S202	Thaum sp. N S202	G. chall N S153	G. chall M. 118324	G. sp. M. 117874
TL (mm)	28.5	48.0	82.0	28.5	92.0	102.0	69.0	372.0	683.0
ML (mm)	8.1	17.0	37.7	13.0	42.0	43.5	26.8	89.5	147.0
MW (mm)	9.2	16.0	38.4	12.0	32.5	32.8	25.9	95.0	154.0
HdL (mm)	5.1	9.1	16.4	6.0	22.0	19.2	12.9	30.5	56.0
HdW (mm)	9.6	16.1	31.0	10.2	34.0	31.0	24.8	82.0	110.0
ED (mm)	5.1	9.8	15.0	5.1	20.2	19.0	12.9	30.5	56.0
EO (mm)	1.1	1.7	3.4	1.5	5.8	8.0	3.0	16.4	24.0
AL1R (mm)	12.0	25.0	49.0	15.8	49.0	53.0	43.0	258.0	550.0
AL2R (mm)	12.0	25.0	48.0	15.5	49.0	53.0	45.0	251.0	546.0
AL3R (mm)	10.5	25.0	51.0	14.8	41.5	44.0	47.0	201.0	455.0*
AL4R (mm)	12.5	24.0	52.0	14.5	52.0	55.0	42.0	223.0	435.0
AF	4.1=2.3	1=2=3.4	4.3.1.2	1.2.3.4	4.1=2.3	4.1=2.3	3.2.1.4	1.2.4.3	1.2.3.4
ASC1R	24	29	35	22	30	30	48	88	98
ASC2R	24	28	35	23	31	32	49	86	99
ASC3R	21	26	36	18	17	20	53	49	*
ASC4R	23	25	37	19	31	31	51	87	96
ASIn1R (%)	0.8	1.0	2.6	0.9	2.1	2.0	1.1	4.8	9.6
ASIn2R (%)	0.8	1.0	2.6	0.9	2.2	2.1	1.1	5.0	9.9
ASIn3R (%)	0.8	1.0	2.9	0.9	2.2	2.2	1.0	5.2	10.4
ASIn4R (%)	0.8	1.0	2.9	0.9	2.1	2.1	1.0	5.5	10.4
GiLC	4/5	5/5	5/5	5/5	5/5	5/5	6/6	6/6	7/7

TL: total lenght, ML: mantle length, MW: mentle width, HdL: head length, HdW: head width, ED: eye diameter, EO: eye orifice width, AL: arm length, 1–4R: right Arm I–right Arm IV, ASC: arm sucker count, ASIn: arm sucker index, GiLC: gill lamellae count, (S): syntypes, (T): holotype, *: broken.

viscera, in the form of a thin muscular riblet running free of the visceral surface and attached to the ventral surface of mantle musculature.

Alimentary canal

The alimentary canal of these larvae is unique in several features (Fig. 3). The anterior salivary glands could not be located, although they may have been damaged or undeveloped in dissected larvae. The digestive gland is, relative to the entire alimentary system, disproportionately large, somewhat elongate and constricted in shape laterally. The colour of the digestive gland is yellow, the contents granular in nature and the gland appears to be full of yolk. Anatomical characters more typical of graneledonine octopods include a narrow oesophagus, no diverti-

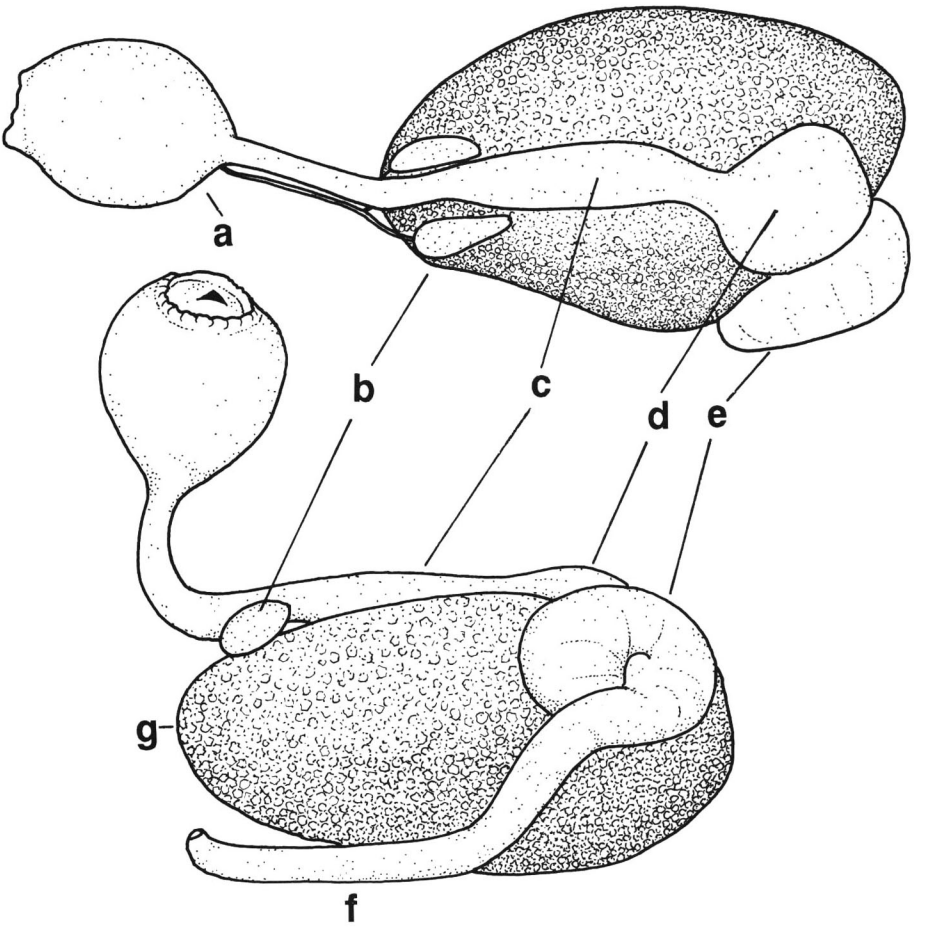

Fig. 3. Alimentary canal of *Graneledone* sp. larva, NMNZ M.119219. a: buccal mass, b: posterior salivary glands, c: crop, d: stomach, e: caecum, f: intestine, g: yolk.

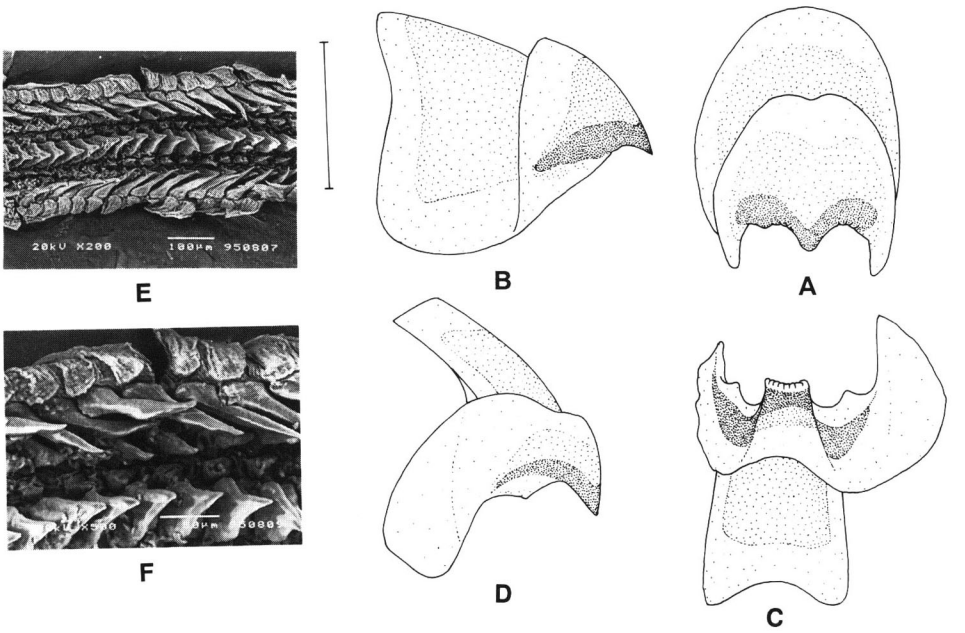

Fig. 4. Beak and radula structures of *Graneledone* sp. larvae. A–B: upper beak, C–D: lower beak (NMNZ M. 119219, scale bar=1mm), E–F: SEM radula (NSMT-Mo98176).

culum of the crop, two vestigial and elyptical-shaped posterior salivary glands, a comparatively large stomach, a spiral caecum without apparent spiral volutions, and an intestine of absolute length equivalent to, or slightly less than the length of the anterior alimentary canal (from eosophagus to stomach). The intestine shows no trace of modification in the form of distensions or constrictions. Both ink sac and anal flaps are absent.

The lower beak (Fig. 4: A, B) is unique amongst adult graneledonine octopods in possessing a strong posterior hood notch and bifid, crenulate rostral tip. Chitonsation is restricted primarily to areas of the rostrum and wing shoulder ridges. The wings, posterior portion of hood and lateral walls of the beak are either translucent or poorly chitonized. The upper beak (Fig. 4: C, D) is more typical of graneledonine octopods in having a weak hood notch, dark pigmented jaw edge and a non-bifid, slightly rounded rostrum.

The radula (Fig. 4: E, F) consists of seven well developed rows of teeth and moderately well-developed marginal plates. The rachidian tooth is fully formed, broad-based and either unicuspid or with a trace of a single basal prominance. Both first and second lateral teeth each have a single cusp, the second lateral also with a broad base. The marginal teeth are comparatively large and robust.

Discussion

The larvae share in common with the genera *Graneledone*, *Thaumeledone* and *Bentheledone* the suckers disposed in a single row along the arms and the absence of an ink sac. Two of these genera, *Graneledone* and *Thaumeledone*, previously have been described from New Zealand waters (HOYLE, 1885, BERRY, 1914, KUBODERA, 1990, O'SHEA, 1990) and all three are recognised from the Southern Ocean (VOSS, 1976, VOSS, 1988b). No specimens of *Bentheledone* are recognised amongst comprehensive collections of bathyal and abyssal octopus species from New Zealand (O'SHEA, pers. obs.). At present this genus is known only from southern ocean abyssal specimens (VOSS, 1988b).

The second set of eggs containing larvae from the Chatham Rise (NMNZ M.119219) are slightly larger than those of ROBSON's 'Type B' and the set of eggs from the Challenger Plateau (NMNZ M.119218). Arm sucker counts in the larvae (NMNZ M.119219), 32–45, differ considerably from those of the comparable sized syntype of *Thaumeledone brevis*, 21–24, and New Zealand juvenile *Thaumeledone* sp. (NZOI Stn S202), 19–23, and from larger New Zealand *Thaumeledone* sp. (NZOI Stn S202), 30–32. Arm sucker counts in juvenile and mature specimens of *Graneledone challengeri* number 48–53 (NZOI Stn S153) and 86–88 except hectocotylized arm of 49 (NMNZ M.18324), respectively (Table 2). Arm sucker counts in the larvae exceed enumerated counts in both comparable-sized and mature specimens of *Thaumeledone* but are slightly lower than those of juvenile *Graneledone*. In both *Thaumeledone* and *Graneledone* arm sucker counts increase with mantle length. Although sucker counts of the larvae exceed ontogenetic ranges in species of *Thaumeledone*, they appear consistant with an apparent ontogenetic range in species of *Graneledone*.

The anatomy of the larvae further distinguishes them from species in the genus *Thaumeledone*. Although both *Graneledone* and *Thaumeledone* are diagnosed as having vestigial posterior salivary glands (VOSS, 1988a), an examination of both the type series of *T. brevis* and additional New Zealand *Thaumeledone* material indicates these glands are, to the contrary, large (O'SHEA, unpub.). Both size and configuration of these glands in the larvae are consistent with those in the genus *Graneledone*.

The genus *Bentheledone* could be excluded from comparison with the larvae on both biogeographic and bathymetric grounds. Two described and two undescribed species are recognised (*fide* VOSS, 1988b), however, none are adequately known to enable any detailed comparison with the larvae described herein. What little is known of species in this genus, the smooth body and the comparatively reduced radula cited as diagnostic (VOSS, 1988a) serves to distinguish the larvae described herein from species in this genus.

Mature ovarian eggs of *Thaumeledone gunteri* measure 5.5×2.5 mm

(ROBSON, 1932: 317) and 16 mm in *Bentheledone rotunda* Hoyle (HOCHBERG *et al.*, 1992). Egg capsule dimensions of NMNZ M.119219 exceed mature ovarian egg sizes in both *Thaumeledone* and *Bentheledone.*

Of the three genera sharing the character combination of uniserial suckers and absence of an ink sac, the larvae from one cluster of eggs (NMNZ M.119219) most closely approximate species recognised in the genus *Graneledone.* Although true cartilage was not detected during mantle tissue staining of the larvae, the composition of these clusters may be similar to the cartilage-like elements on the ventral mantle surfaces in the genus *Ocythoe* in not being true-cartilage (*fide* NAEF, 1923).

Those eggs previously described proximal to New Zealand (ROBSON, 1932) and the smaller egg cluster from the Challenger Plateau (NMNZ M.119218) described herein are of a similar dimension, *ca* 20–22 mm in capsule length, and the external facies are essentially identical. In the absence of larvae within the egg capsules, and because species of *Benthoctopus* and *Graneledone* have similar sized mature ovarian eggs (*fide* HOCHBERG *et al.*, 1992; pers. obs.), it cannot be discounted that NMNZ M.119218 and 'Type B' eggs of Robson are those of a species of *Benthoctopus.* The gross similarity between these sets of eggs, however, makes *Graneledone* the most likely candidate.

Acknowledgements

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