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ORIGINAL PAPER

Two new 'bottletail squids' (Cephalopoda: Sepiadariidae: *Sepioloidea*) from New Zealand, with new observations on *Sepioloidea pacifica* (Kirk, 1882)

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Abstract

Members of the cephalopod family Sepiadariidae Fischer, 1882, commonly called 'bottletail squids', are known primarily from the Indo-Pacific and southwest Pacific. To date, only one species is known to occur in New Zealand waters: *Sepioloidea pacifica* (Kirk, 1882). However, researchers have long suspected the presence of additional species in the genus *Sepioloidea* d'Orbigny, 1845 in Férussac & d'Orbigny 1835-1848. The majority of known *Sepioloidea* material from New Zealand national collections was examined; both morphological and, where available, molecular characters are compared. As a result, two new species, *Sepioloidea virgilioi* sp. nov. and *Sepioloidea jaelae* sp. nov., are recognised and described. Diagnostic morphological characters include the tentacular club sucker arrangement and hectocotylus structure. Molecular data support the recognition of these two new taxa, with sampled populations of each of the three available *Sepioloidea* falling within three monophyletic clades following analysis of COI (cytochrome *c* oxidase subunit I) sequence data. The minimum interspecific distance is 11.09%—far greater than the maximum intraspecific distance (1.57%). A revised diagnosis for *S. pacifica* sensu stricto is also provided.

Keywords Sepiolida · Taxonomy · Southwest Pacific · DNA barcode · COI

Introduction

The cephalopod genus *Sepioloidea* d'Orbigny, 1845 in Férussac & d'Orbigny 1835-1848, is primarily known from Australasian waters, with one nominal species reported from New Zealand: *Sepioloidea pacifica* (Kirk, 1882). However, cephalopod researcher Dr Steve O'Shea recognised the presence of additional species housed in national collection facilities such as the Museum of New Zealand Te Papa Tongarewa (NMNZ) and the National Institute of Water and Atmospheric Research, Ltd (NIWA). These specimens have not been examined in detail until now to formally determine species boundaries, and in the interim, many specimens have been attributed by default to *S. pacifica.* One potentially novel taxon was initially recognised as a subject of taxonomic interest due to the relatively large size of mature specimens (up to three times the average mantle length of mature *S. pacifica*), and its occurrence in deep water. Another was recognised due to unique tentacle-club morphology and opportunistic genetic sequencing. These specimens have often been informally designated within collections conservatively as '*Sepioloidea* sp. nov.' or 'Sepiolida' until detailed study and comparison with other described sepiadariids could be undertaken.

Preliminary examinations revealed additional morphological characters that were consistently different from the other known *Sepioloidea* species—*S. lineolata* (Quoy & Gaimard, 1832), *S. pacifica*, and *S. magna* Reid, 2009—indicating that more detailed investigation was, indeed, warranted. An integrative taxonomic approach was adopted for this investigation, combining molecular (cytochrome *c* oxidase subunit I [COI]) and morphological evidence to review the true diversity represented by *Sepioloidea* found in New Zealand waters.

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To facilitate direct comparisons among taxa, a revised diagnosis for *S. pacifica* is provided, with additional information reporting details of traits not already included in existing taxonomic literature (Dell 1952, 1959; Kirk 1882). In addition, aspects of the biology of the poorly known Sepiadariidae are discussed as inferred from studies of representatives of its sister taxon, the Sepiolidae.

Material and methods

Specimens

Preserved *Sepioloidea* specimens were loaned from NMNZ and NIWA, both in Wellington, New Zealand; the Auckland War Memorial Museum (AWMM) in Auckland, New Zealand; and the Australian Museum (AM) in Sydney, Australia. Other depositories mentioned include the Museum and Art Gallery Northern Territory (NTM). Collection depths for each specimen lot are given where available. When a depth range is given, specimens may have been collected at any depth covered within the range. Single depth values refer only to an accurate collection depth if an opening-closing net was used and this information was not always available. The exact collection method is not always included with the specimen collection data, and there is no clear distinction between bottom depth and operational trawling/towing depth. In total, 610 preserved specimens were examined, and an additional 61 frozen specimens were sequenced (with those of suitable condition also morphologically examined and identified where possible). The collection locations represent broad coastal coverage of the New Zealand land mass, and some offshore locations (Fig. 1). Specimens previously identified as *Sepioloidea pacifica* were compared with the neotype and earlier descriptions. All specimens belonging to the family Sepiadariidae were selected for examination with

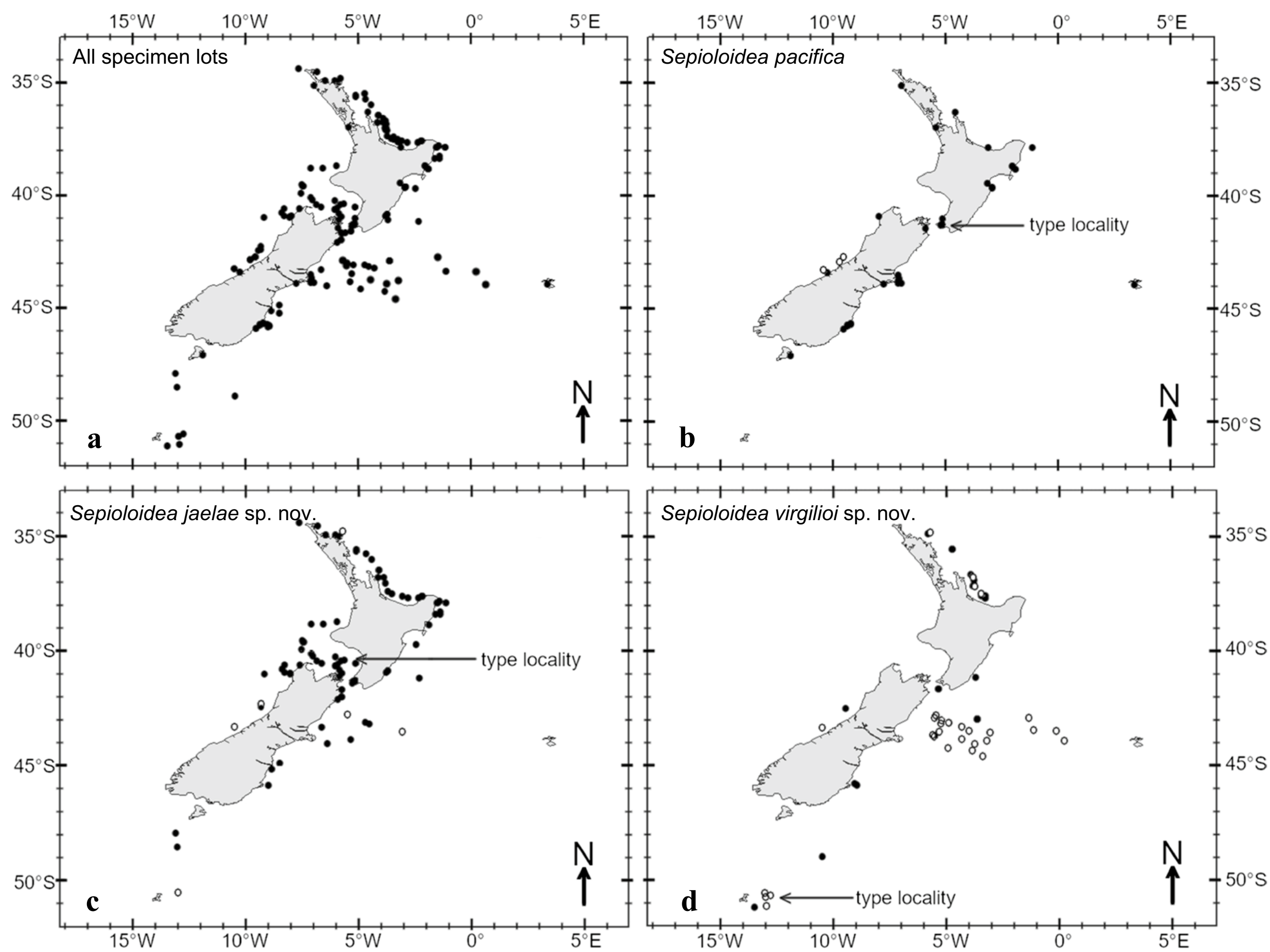

Fig. 1 Collection locations of New Zealand *Sepioloidea* specimen lots examined in this study including sequenced (hollow circles) and non-sequenced (filled circles) specimens: **a** all specimen lots; **b** *Sepioloidea pacifica*; **c** *Sepioloidea jaelae* sp. nov.; **d** *Sepioloidea virgilioi* sp. nov.

those in the best condition examined in detail to prepare descriptions and identify reliable characters that could be used for differentiating hypothesised species.

Collection dates are given in the format dd/mm/yyyy (e.g., 31/01/2000), or mm/yyyy. Where specimen lot latitude and longitude data had to be estimated, co-ordinates were estimated using Google Earth. Illustrations and schematic drawings were drawn either by hand or created using the 'GNU Image Manipulation Program (GIMP)' version 2.10.12 software. All image editing was processed in GIMP. Distribution maps were created with ArcGIS (Environmental Systems Research Institute [ESRI], Redlands, CA).

Morphology

Morphological examination focused primarily on external anatomy, with some internal characters assessed where possible. Terminology for anatomical structures followed Roper and Voss (1983) with notes on any additions and changes listed in Table 1. Following Reid (2009), this study adopted the measurement of 'Fin Insertion anterior' (FIa) and the definition of the 'Arm Sucker Count' (ASC). Due to the unreliable nature of finding a halfway measure, ASC in this paper refers to the total number of suckers along an arm rather than along the basal half as in Roper and Voss (1983). Additionally, due to the elastic nature of tentacles (and the delicate process of extracting retracted tentacles from the tentacular pocket), their lengths were deemed unreliable measurements and therefore not included. Measurements were based on 10 mature specimens of each sex where possible; where damaged specimens have been excluded from a measurement, the new sample size is given as ($n = $x). Ranges of indices are given in the format x–*y*–z where x and z are the minimum and maximum observed values, respectively, and *y* is the mean. All intact mature specimens were sexed while those that were too damaged to be determined are instead labelled 'indet.'. Specimens with mantles in poor condition (e.g., some frozen material used for DNA sampling) were not measured for mantle length. All measurements are given in millimetres (mm). In the material examined sections, * indicates specimen lots that have been sequenced; ^ indicates specimen lots with GPS coordinates estimated from locality descriptors. Depths from these ^ specimen lots were not estimated but only given if explicitly recorded on the label.

In preparation for scanning electron microscopy (SEM), tentacle clubs and radulae were critical-point dried. Radular tooth terminology follows Reid (2009). Arm suckers were air dried for at least 24 h in a lightly sealed box containing silicone dessicant. All specimens were mounted, plated with platinum, and imaged with a Hitachi SU-70 SEM operated at 5 kV. Beaks were described following Clarke (1986) and drawn from photographs. Arm and tentacular sucker descriptions and terminology were based on Salcedo-Vargas (1995).

Spermatophores were obtained from mature male specimens. Those closest to the genital opening were extracted and mounted on microscope slides in glycerine for examination using a compound microscope.

Specimens examined in this study varied greatly in condition, with some having been frozen and thawed following collection, and some suffering net damage. Therefore, while the best-quality morphological vouchers were selected, measurements may not precisely reflect those of live or fresh individuals.

DNA barcoding

Tissue samples were obtained from 61 frozen or ethanol-fixed specimens. Formalin-fixed specimens were not used for the genetic analysis due to the extreme difficulty of recovering DNA from such material. Small tissue samples of mantle or fin tissue were subsampled (~ 1–3 mm^3). These tissue snips were kept frozen at − 20 °C until DNA extraction, or fixed in either 100% or 80% ethanol and stored at room temperature. These specimens were examined to determine congruence with morphological patterns observed among preserved material.

DNA was extracted using EconoSpin (Epoch Life Science) spin columns with QIAGEN reagents following the protocols for the DNeasy Blood and Tissue Kit (QIAGEN). The DNA barcode region (648 bp from the 5' end of the mitochondrial gene COI) was amplified using Folmer et al. (1994) primers LCO1490/HCO2198. Polymerase chain reaction (PCR) was undertaken in 12.5 µL reaction volumes with: 6.25 µL 10% trehalose, 2 µL double distilled H_2O, 1.25 µL 10 × buffer, 0.625 µL $MgCl_2$ (50 mM), 0.1 µL LCO1490 (10 µm), 0.1 µL HCO2198 (10 µm), 0.0625 µL 10 mM deoxynucleoside triphosphate (dNTP), 0.06 µL Platinum Taq polymerase (5 U/µL), and 2 µL of DNA. The thermocycle reaction profile was as follows: hot start of 94 °C for 1 min; 5 cycles, each with 94 °C for 40 s, 45 °C for 40 s, 72 °C for 1 min; 35 cycles, each with 94 °C for 40 s, 51 °C for 40 s, 72 °C for 1 min; extension at 72 °C for 5 min, and held at 4 °C indefinitely.

The amplification success of PCR products was ascertained visually using a 1% agarose gel stained with GelRed (Biotium). A single, clear band on the gel indicated successful amplification. Amplified samples were sequenced by Macrogen (Korea) using the same primers used for PCR. Bidirectional sequences were assembled into contigs and edited in CodonCode Aligner v.9.0.1 software (CodonCode Corporation). Sequences were aligned using Multiple Alignment using Fast Fourier Transform (MAFFT) (https://www.ebi.ac.uk/Tools/msa/mafft/) and uploaded to the Barcode

Table 1 Description of measurements, counts, and abbreviations (Abb.) following Reid (2009), metrics from Roper and Voss (1983) indicated by [*RV*], new or altered metrics indicated by an asterisk (*). Indices are shown in square brackets and are calculated as a percentage of mantle length. HcMLI is calculated as a percentage of hectocotylus length

Feature	Abb	Description	Feature	Abb	Description
Arm length	AL	Length of arm measured from first basal (proximal-most) sucker to tip of arm (Arm I, dorsal; II, dorso-lateral; III, dorso-ventral; IV, ventral). [**ALI**]	Funnel length	FuL	Length of funnel from anterior funnel opening to posterior margin measured along ventral midline. [**FuLI**]
Arm sucker count	ASC	Total number of suckers on each designated arm (e.g., ASC1 for the total count on Arms I)	Head length*	HL	Dorsal length of head measured from point of fusion of dorsal arms to anterior midpoint of junction between head and mantle. [**HLI**]
Arm sucker diameter	AS	Diameter of largest normal sucker on each designated arm. [**ASIn**]	Head width	HW	Greatest width of head at level of eyes. [**HWI**]
Club length	ClL	Length of tentacular club measured from proximal-most basal suckers to distal tip of club. [**ClLI**]	Hectocotylus lappet pair count*	HcLPC	Number of lappet pairs on hectocotylised arm.
Club row count	ClRC	Number of suckers in transverse rows on tentacular club.	Hectocotylus length*	HcL	Length of hectocotylus measured from basalmost sucker to distal tip. [**HcLI**]
Club sucker diameter	ClS	Diameter of largest sucker on tentacular club. [**ClSI**]	Hectocotylus modification length*	HcML	Length of modified section of hectocotylus. [**HcMLI**] (as a percentage of hectocotylus length)
Egg diameter	EgD	Diameter of largest egg present in ovary or oviduct. [**EgDI**]	Hectocotylus sucker count*	HcSC	Total number of suckers on hectocotylus.
Eye diameter*	ED	Diameter of eye opening. [**EDI**]	Hectocotylus sucker diameter*	HcS	Diameter of largest sucker on hectocotylus. [**HcSI**]
Fin insertion	FI	Length of fin as joined to mantle. [**FII**]	Mantle length	ML	Dorsal mantle length. Measured from anterior-most point of mantle to posterior apex of mantle
Fin insertion anterior	FIa	Anterior origin of fin measured from mantle margin to anterior-most junction of fin and mantle. [**FIIa**]	Occipital band width	OBW	Minimum width of band of skin that joins head to mantle. [**OBWI**]
Fin width	FW	Greatest width of single fin. [**FWI**]	Spermatophore length [*RV*]	SL	Longest developed spermatophore in Needham's sac. [**SLI**]
Free funnel length	FFu	Length of the funnel from the anterior funnel opening to point of dorsal attachment to the head. [**FFuI**]			

of Life Data System (BOLD) (Ratnasingham and Herbert 2007) in a public project titled 'New Zealand Sepiolids' (project code: NZSEP). Sequences were screened for contamination using the Basic Local Alignment Search Tool (BLAST) through GenBank.

Sequences were compared with those from *S. lineolata* (GenBank accession numbers AF000064 and LC417220), the only other sequenced nominal *Sepioloidea* species (sequences for *S. magna* are not currently available). The outgroup species, *Rossia pacifica* Berry, 1911 (GenBank accession number GU802389.1), was chosen because the family to which it belongs (Sepiolidae) appears to have a sister-group relationship with Sepiadariidae (Groenenberg et al. 2009; Sanchez et al. 2021).

Taxonomy

Sepioloidea pacifica (Kirk, 1882)
(Figs 1–3, 16, 17; Tables 7, 8).
Sepiola pacifica Kirk, 1882: 283–284.
Sepioloidea pacifica (Kirk, 1882): Dell 1952: 82–87, tables 21–23, Fig. 5, pl. 33–35; Dell 1959: 2–3 (in part); Hurst 1969 (in part); Powell 1979: 440 (in part).

Type material examined: New Zealand: *Neotype* Dell (1959): 1♀, 21 mm ML (NMNZ M.12954^) 41° 15′ 30″ S, 174° 55′ 0″ E, 24/05/1953, Coll. J. Moreland.

Other material examined: New Zealand: 3♀, 20–21 mm ML (NIWA 142282) 35° 7′ 12″ S, 173° 5′ 35″ E, 24 m, 05/02/1977, Coll. NZOI, Stn P58; 1♀, 12 mm ML (NMNZ M.012960^) 36° 19′ 27″ S, 175° 27′ 55″ E, 14/05/1954, Coll. W. Sampson on FV *Zyder Zee*; 1♂, 14 mm ML (NMNZ M.074121) 36° 45′ 0″ S, 175° 4′ 0″ E, 26–31 m, 10/10/1965, RV *Ikatere*; 2♀, 21–22 mm ML (NMNZ M.287469) 37° 0′ 0″ S, 174° 36′ 30″ E, 3 m, 27/04/1994, Coll. S. J. O'Shea on RV *Tangaroa*; 1♀, 20 mm ML (NMNZ M.287397) 37° 51′ 24″ S, 178° 54′ 36″ E, 30 m over 904 m, 18/04/1980, RV *James Cook*, Stn J08/05/80; 5♂, 8–16 mm ML (NMNZ M.074214) 37° 51′ 48″ S, 176° 56′ 48″ E, 34–39 m, 21/01/1979, RV *Tangaroa*, Stn 1979728; 11♂, 9–14 mm ML (NMNZ M.067236) 2♂, 8–14 mm ML (NMNZ M.067308): 38° 42′ 10″ S, 178° 0′ 41″ E, 18–26 m, 09/01/1980, RV *James Cook*, Stn J01/01/80; 1♀, 17 mm ML (NMNZ M.287491) 38° 43′ 18″ S, 178° 1′ 42″ E, 20 m over 21 m, 19/02/1984, RV *James Cook*, Stn J04/12/84; 1♂, 10 mm ML (NMNZ M.067316) 38° 49′ 35″ S, 178° 8′ 29″ E, 29 m over 47–89 m, 09/01/1980–10/01/1980, RV *James Cook*, Stn J01/02/80; 1♂, 12 mm ML (NMNZ M.067297) 38° 50′ 12″ S, 178° 9′ 12″ E, 30 m, 18/11/1979, RV *James Cook*, Stn J16/02/79; 1♂, 12 mm ML (NMNZ M.006297) 39° 27′ 30″ S, 176° 54′ 0″ E, 15 m, 21/05/1952, MV *Kotuku*, Stn 1952155; 12♂, 15–17 mm ML (NMNZ M.287488) 39° 38′ 37″ S, 177° 7′ 35″ E, 51–52 m, 22/06/1983, FV *Kalinovo*, Stn K11/001/83; 7♂, 11–15 mm ML (NMNZ M.287492) 39° 39′ 33″ S, 177° 5′ 58″ E, 12 m, 22/06/1983, FV *Kalinovo*, Stn K11/004/83; 1♀, 18 mm ML (NMNZ M.074124) 40° 54′ 0″ S, 172° 4′ 0″ E, 55 m, 10/03/1976, RV *Acheron*, Stn 1976530; 10♂, 15–19 mm ML (NMNZ M.074223) 41° 2′ 0″ S, 174° 54′ 0″ E, 50 m, 25/05/1970, Coll. E. K. Saul; 2♀, 15–17 mm ML (NMNZ M.012955) 41° 15′ 30″ S, 174° 54′ 0″ E, 24/05/1953, Coll. J. M. Moreland; 1♀, 25 mm ML (NMNZ M.012956) 41° 15′ 30″ S, 174° 55′ 0″ E, 0 m, 14/07/1954, Coll. J. C. Yaldwyn; 3♂, 15–17 mm ML, 6♀ 11–26 mm ML (NMNZ M.287498^) 41° 16′ 21″ S, 174° 51′ 26″ E; 1♂, 19 mm ML (NMNZ M.287504) 41° 17′ 53″ S, 174° 50′ 04″ E, 5 m, 14/06/1983, Coll. A. L. Stewart, G. S. Hardy; 2♂, 15–17 mm ML (NMNZ M.074215) 41° 27′ 0″ S, 174° 8′ 36″ E, 27–28 m, 28/01/1979, RV *Tangaroa*, Stn 1979775; 1 indet. (NIWA 142703*) 42° 49′ 31″ S, 170° 29′ 43″ E, 43–47 m, 09/04/2019, RV *Kaharoa*, Stn KAH1902/63; 8 indet. (NIWA 142704*) 42° 56′ 34″ S, 170° 26′ 19″ E, 31–32 m, 09/04/2019, RV *Kaharoa*, Stn KAH1902/64; 7♀ (NIWA 142705*) 43° 27′ 4″ S, 169° 36′ 32″ E, 45–48 m, 12/04/2019, RV *Kaharoa*, Stn KAH1902/69; 1♂, 19 mm ML, 2♀, 20–24 mm ML (NIWA 142283) 43° 31′ 52″ S, 172° 56′ 46″ E, 25–26 m, 12/12/1996, Coll. NIWA, MFish on RV *Kaharoa*, Stn KAH9618/1; 10♂, 14–16 mm ML, 1♀, 20 mm ML (NMNZ M.005631 [Vouchers, Dell (1952)]) 43° 38′ 26″ S, 172° 57′ 57″ E, 0 m, 1949, Coll. E. Percival, G. A. Knox; 1♂, 15 mm ML (NMNZ M.287511) 43° 47′ 0″ S, 172° 56′ 0″ E, 5 m, 27/09/1976, RV *Acheron*, Stn 1976552; 2♀, 16–18 mm ML (NMNZ M.074131) 43° 51′ 30″ S, 172° 55′ 30″ E, 15 m, 27/09/1976, RV *Acheron*, Stn 1976553; 1♀, 20 mm ML (NMNZ M.090341) 43° 52′ 0″ S, 173° 6′ 0″ E, 44 m, 27/09/1976, RV *Acheron*, Stn 1976556; 1♀, 24 mm ML (NIWA 84786) 43° 53′ 35″ S, 172° 17′ 24″ E, 13 m, 17/12/1999, Stn Z9964; 1♀, 15 mm ML (NMNZ M.013470^) 43° 56′ 49″ S, 176° 33′ 03″ W, 29/01/1954, MV *Alert*; 2♂, 16–17 mm ML (NMNZ M.011032) 45° 40′ 0″ S, 170° 51′ 0″ E, 37 m, 13/01/1957, MV *Alert*, Stn 1957198; 1♂, 11 mm ML (NMNZ M.074092) 45° 41′ 41″ S, 170° 48′ 56″ E, 33 m, 04/03/1930, Coll. D. H. Graham; 1♀, 16 mm ML (NMNZ M.287406) 45° 43′ 0″ S, 170° 42′ 0″ E, 27 m, 04/1975, RV *Acheron*; 3♀, 7–14 mm ML (NMNZ M.008859) 45° 43′ 47″ S, 170° 41′ 31″ E, 22 m, 27/06/1954, MV *Alert*; 3♂, 6–15 mm ML, 1♀, 15 mm ML, 1 indet., 4 mm ML (NMNZ M.011039) 45° 53′ 08″ S, 170° 30′ 57″ E, 0 m, 21/01/1979, Coll. R. K. Dell, J. M. Moreland; 4♂, 9–15 mm ML (NMNZ M.074222) 47° 3′ 54″ S, 168° 10′ 0″ E, 0 m, 02/03/1972, Coll. J. M. Moreland; 1♀, 15 mm ML (NMNZ M.287505) 1982, RV *James Cook*, Stn J16/94/82.

Diagnosis: Mantle length up to 19 mm in mature males and 26 mm in mature females. Anterior mantle margin smooth, without fringing projections. All arm suckers

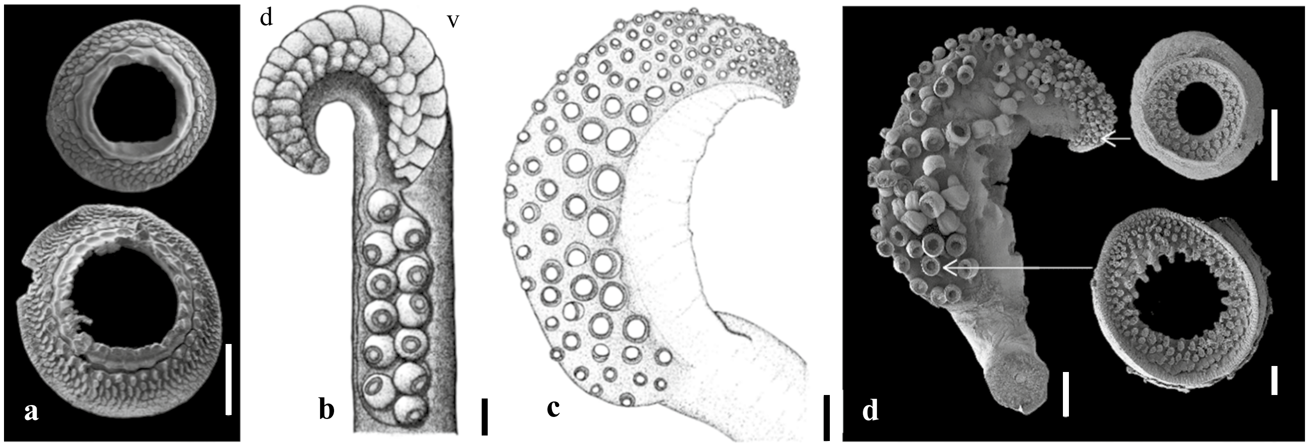

Fig. 2 *Sepioloidea pacifica*: **a** SEM images, upper, right Arm IV sucker, NMNZ M.074214, ♂, 14 mm ML; lower, right Arm I sucker, NMNZ M.012955, ♀, 17 mm ML; **b** hectocotylised left Arm IV, oral view, NMNZ M.005361, ♂, 16 mm ML; **c** right tentacular club, NMNZ M.012955, ♂, 17 mm ML; **d** SEM images right tentacular club (left image) and club suckers (right images), NMNZ M.012955, ♀, 17 mm ML. Abbreviations: *d*, dorsal; *v*, ventral. Scale bars a, 100 µm; b, 600 µm; c, 300 µm; d, club 500 µm, suckers 50 µm

biserial throughout. Arm suckers decrease in size from base to distal arm tip; minor enlargement of suckers midway along Arms I in males. Ventral left arm hectocotylised; distal ~ 50% of arm modified; basal unmodified section with ~ 6 sucker pairs. Modified section of hectocotylus curved, without suckers but with sucker pedicels joined basally and modified forming ~ 20 lappets; each lappet wedge-like ventrally, bilobed dorsally. Tentacular club suckers in transverse rows of approximately five; suckers noticeably largest midway along dorsal club margin. Chromatophores relatively large, pale, irregular-shaped spots, interspersed with smaller, darker spots; no stripes [modified from Dell (1952)].

Additional information: Eyes large, occupying significant portion of head; aperture covered by transparent membrane. Female arm suckers largest basally, uniformly decreasing in size distally. Male Arms I differ with suckers slightly enlarged mid-arm. Arm sucker ring sizes similar between sexes; infundibulum primarily smooth in males, slightly crenulated in females (Fig. 2a). Papillated portion with about four concentric rings of polygonal processes. Internal ring consists of ~ 21–32 pentagonal polygonal processes; inner margin flat, outer margin pointed. Each process with ridge-like peg extending medially from inner to outer margins; ridge either straight or crescentric. Intermediate rings with ~ 35–70 flat, scale-like, polygonal processes that decrease in size and increase in number towards outer ring margins. Intermediate ring polygonal processes with pegs in females; smooth in males. Hectocotylus sucker rims do not differ from those on opposite right Arm IV. Sucker rim ultrastructure does not differ along the length of the arms.

Left ventral arm of males hectocotylised (Fig. 2b); unmodified proximal section with ~ 6 normal sucker pairs; distal ~ 50% modified. Modified section devoid of suckers; modified sucker pedicel pairs form fused lappets; lappets wedge-like ventrally, bilobed dorsally.

Tentacle stalks long, slender, semi-circular in cross-section, without suckers. Clubs (Fig. 2c, d) expanded, tapering to a blunt tip. About five suckers per transverse row, set on short pedicels. Suckers usually largest along medial 25–50% of club dorsal margin; distal-most suckers markedly smaller than remaining suckers. Dorsal keel extends slightly beyond sucker-bearing face of club. Tentacle suckers (Fig. 2d) with irregular ovoid pegs. Pegs widely spaced; underlying polygonal processes visible between pegs; peg surfaces pitted. Proximal suckers asymmetrical; pegs in up to seven intermediate rings, distal pegs elongate, proximal pegs short and blunt. Distal suckers symmetrical; pegs in about four intermediate rings and consistent in shape. Internal ring consists of ~ 13 pegs, external ring with ~ 40–60 pegs.

Preserved specimen colouration varies from pale cream to dark brown. Chromatophores (Fig. 3a) include both tiny dots and larger spots, dark brown/purple, evenly distributed across dorsal surface of mantle, fins, head, and along Arms I–III; sparsely concentrated on ventral surfaces of the mantle, fins, head, and along Arms IV. Chromatophores present on aboral surface of tentacle club; small and densely set near tip, larger and very sparse proximally, extending along stalk for 150% club length.

Type locality: Lowry Bay, Wellington Harbour, Wellington, New Zealand, 41° 15′ 30″ S, 174° 54′ 30″ E, 0 m [otter trawl].

Distribution (Fig. 1b): Southwest Pacific, New Zealand including Chatham Islands; 0–55 m.

Remarks: Morphological differences between *S. pacifica* and all other recognised *Sepioloidea* are highlighted in the Remarks after each species description below and

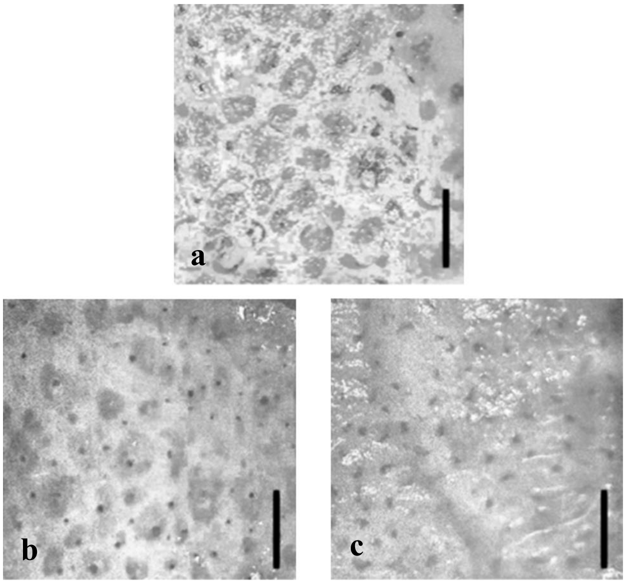

Fig. 3 Dorsal mantle chromatophore arrangement in preserved specimens: **a** *Sepioloidea pacifica*, large, pale, irregular-shaped spots and smaller, dark spots; **b** *S. jaelae* sp. nov., large pale spots, and tiny, dark dots; **c** *S. virgilioi* sp. nov., tiny, evenly distributed dots. Scale bars 1 mm

summarised in Table 7. Previous authors have referred to relatively deep-water representatives of this species (e.g., Dell 1959: 2: 'large specimens … from depths greater than 75 fathoms [137 m]'; Hurst 1969: 8: 'However, several trips were also made in to deeper water and on two of these occasions a single deep-water specimen of *Sepioloidea* was collected. These were large forms and were collected from depths of 140 and 210 m'.; Powell (1979): 440: '*Sepioloidea pacifica* … Dunedin Harbour. Off eastern Otago, 75–300 fathoms [137–550 m]'.). It is now known that these references likely refer to other *Sepioloidea* species. Further details of the 'in part' entries in the *S. pacifica* synonymy above are provided in the Remarks sections for *S. jaelae* sp. nov. and *S. virgilioi* sp. nov. below.

A single specimen identified as *Sepioloidea* cf. *pacifica* has also been reported from the Sala y Gómez submarine ridge in the eastern Pacific (Parin et al. 1997, based on Nesis 1990) but could not be examined in this study. The outlying specimen collected from the Chatham Islands has been thoroughly examined and conforms in all traits with *S. pacifica* from the North and South Islands of New Zealand.

Sepioloidea jaelae sp. nov.

http://zoobank.org/EDEDC693-8048-4546-A50B-81EC3653448C
(Figs 1, 3–8, 16, 17; Tables 2, 3, 7, 8).
Sepioloidea pacifica (Kirk, 1882): Powell (1979).
Sepiadariidae sp. Sanchez et al. (2021).

Type material examined: New Zealand: *Holotype*. 1♂, 16 mm ML (NMNZ M.287489) 40° 14′ 24″ S, 174° 0.1′ E, 96–101 m, 20/02/1983, RV *Kaharoa*.

Paratypes. 9♂, 14–16 mm ML (NMNZ M.330524); 5♀, 14–16 mm ML (NMNZ M.330525); 5♀, 12–22 mm ML (NMNZ M.330526): 40° 14′ 24″ S, 174° 0.1′ E, 96–101 m, 20/02/1983, RV *Kaharoa.*

Additional material examined: New Zealand: 1♀, 15 mm ML (NMNZ M.090405) 34° 22′ 48″ S, 172° 24′ 36″ E, 121 m, 02/02/1981, Stn 1981912; 1♀, 16 mm ML (NMNZ M.067326) 34° 32′ 0″ S, 173° 13′ 0″ E, 40 m, 05/07/1977, RV *Ikatere*; 1♂, 13 mm ML (NIWA 55378*) 34° 54′ 36″ S, 174° 0′ 0″ E, 143–149 m, 08/07/2009, Coll. Oceans Survey 2020, Stn TAN0906/78; 1♂, 12 mm ML (NMNZ M.074141) 34° 56′ 0″ S, 173° 34′ 0″ E, 47 m, 18/09/1971, Stn 1971003; 1♂, 13 mm ML (NIWA 142311) 35° 0′ 0″ S, 174° 12′ 0″ E, 175 m, 08/05/1975, Coll. NZOI, Stn I39; 1♂, 13 mm ML, 1♀, 18 mm ML (NMNZ M.074122) 35° 33′ 0″ S, 174° 57′ 0″ E, 183–201 m, 14/02/1974, RV *Acheron*, Stn 1974365/A; 3♀, 13–19 mm ML (NMNZ M.287497) 35° 38′ 0″ S, 174° 56′ 0″ E, 165 m, 20/11/1962, RV *Ikatere*, Stn 1962086; 2♂, 12–14 mm ML (NMNZ M.287503) 35° 44′ 42″ S, 175° 22′ 36″ E, 185 m, 01/06/1982, FV *Kalinovo*; 1♂, 13 mm ML (NIWA 142308) 36° 0′ 0″ S, 175° 37′ 12″ E, 139 m, 13/05/1975, Coll. NZOI, Stn I68; 1♂, 15 mm ML, 9♀, 16–20 mm ML (NMNZ M.074099) 36° 26′ 34″ S, 175° 57′ 03″ E, 159–170 m, 11/11/1964, RV *Ikatere*; 1♀, 18 mm ML (NMNZ M.074118) 36° 26′ 34″ S, 175° 57′ 03″ E, 154 m, 24/11/1965, RV *Ikatere*; 1♂, 10 mm ML (NMNZ M.287395) 36° 45′ 42″ S, 176° 9′ 24″ E, 148 m, 25/02/1981, RV *James Cook*, Stn J04/88/81; 1♂, 11 mm ML (NMNZ M.287507) 36° 46′ 09″ S, 175° 55′ 06″ E, 99–104 m, 24/02/1981, RV *James Cook*, Stn J04/85/81; 3♀, 11–13 mm ML (NMNZ M.287510) 37° 0′ 48′ S, 176° 12′ 18″ E, 178–248 m, 23/01/1979, RV *Tangaroa*, Stn 1979756; 1♂, 11 mm ML (NMNZ M.287512) 37° 21′ 54″ S, 176° 20′ 54″ E, 203–248 m, 22/01/1979, RV *Tangaroa*, Stn 1979743; 1♂, 13 mm ML (NIWA 142272) 37° 29′ 24″ S, 176° 31′ 05″ E, 219–217 m, 20/02/2000, Coll. NIWA, MFish, Stn KAH0001/76; 1♀, 17 mm ML (NMNZ M.067294) 37° 35′ 13″ S, 177° 52′ 55″ E, 30 m over 94 m, 03/11/1979, RV *James Cook*, Stn J15/02/79; 2♂, 10–11 mm ML (NMNZ M.287495) 37° 35′ 48″ S, 177° 49′ 48″ E, 82–109 m, 23/02/1981, RV *James Cook*, Stn J04/70/81; 1♂, 14 mm ML (NMNZ M.287514) 37° 35′ 54″ S, 176° 59′ 30″ E, 139–179 m, 20/01/1979, RV *Tangaroa*, Stn 1979723; 1♂, 9 mm ML (NMNZ M.287396) 37° 39′ 0″ S, 177° 14′ 36″ E, 108 m over 622–820 m, 13/12/1975, RV *James Cook*, Stn J17/51/75; 2♂, 11–12 mm ML (NMNZ M.067288) 37° 39′ 12″ S, 177° 41′ 30″ E, 30 m, 20/11/1979, RV *James Cook*, Stn J16/22/79; 1♂, 14 mm ML (NMNZ M.091694) 37° 48′ 0″ S, 178° 36′ 0″ E, 27 m over 73 m, 18/10/1969–19/10/1969, RV *James Cook*, Stn J06/112/69; 7♂, 8–13 mm ML, 7♀,

Table 2 *Sepioloidea jaelae* sp. nov. type series ♂ specimen counts and measurements

Collection Reg. no. Sex Type	NMNZ M.287489 ♂ Holotype	NMNZ M.330524 ♂ Paratype	NMNZ M.330524 ♂ Paratype	NMNZ M.330524 ♂ Paratype	NMNZ M.330524 ♂ Paratype	NMNZ M.330524 ♂ Paratype	NMNZ M.330524 ♂ Paratype	NMNZ M.330524 ♂ Paratype	NMNZ M.330524 ♂ Paratype	NMNZ M.330524 ♂ Paratype
ML	16.0	14.0	14.0	14.0	15.0	15.0	15.0	15.0	16.0	16.0
MWI	87.5	85.7	85.7	85.7	73.3	86.7	80.0	93.3	81.3	75.0
FWI	31.3	21.4	28.6	21.4	20.0	20.0	20.0	20.0	18.8	18.8
FIIa	25.0	28.6	35.7	28.6	26.7	26.7	26.7	40.0	25.0	25.0
FII	50.0	42.9	42.9	42.9	40.0	40.0	33.3	46.7	31.3	37.5
FuLI	50.0	50.0	64.3	57.1	53.3	60.0	53.3	53.3	50.0	50.0
FFuI	18.8	21.4	28.6	21.4	20.0	26.7	20.0	26.7	18.8	18.8
HLI	62.5	64.3	64.3	64.3	60.0	60.0	53.3	66.7	56.3	50.0
HWI	81.3	71.4	92.9	71.4	73.3	73.3	73.3	86.7	68.8	68.8
EDI	18.8	14.3	14.3	21.4	20.0	20.0	20.0	20.0	18.8	25.0
OBWI	67.9	48.4	48.5	36.4	48.5	46.7	34.5	42.3	33.3	43.3
AL1I	75.0	71.4	64.3	71.4	73.3	66.7	66.7	66.7	62.5	68.8
AL2I	81.3	64.3	71.4	85.7	80.0	73.3	66.7	73.3	62.5	75.0
AL3I	75.0	71.4	78.6	85.7	80.0	66.7	73.3	73.3	68.8	75.0
AL4I	75.0	71.4	78.6	85.7	73.3	73.3	73.3	73.3	75.0	75.0
ASIn1	5.1	5.2	5.1	5.4	4.5	4.3	4.3	5.1	4.6	4.3
ASIn2	5.2	5.6	6.1	5.6	5.4	5.0	4.6	4.8	4.7	4.9
ASIn3	5.9	6.0	5.9	5.9	5.8	5.1	5.1	5.0	5.1	4.8
ASIn4	6.1	5.8	5.5	5.9	5.1	5.2	4.9	5.0	4.8	4.4
ASC1	32	28	30	30	26	30	27	24	28	32
ASC2	31	24	28	30	27	28	24	28	30	30
ASC3	31	30	32	34	34	30	26	30	32	38
ASC4	31	29	24	32	32	35	26	34	32	32
ClLI	25.0	28.6	28.6	28.6	20.0	26.7	20.0	20.0	25.0	25.0
ClRC	5	5	6	6	6	6	6	7	5	6
TIRC	24	23	27	26	26	26	22	22	26	24
ClSI	1.3	1.2	1.4	0.9	1.3	1.1	1.2	0.8	0.9	1.3
HcLI	81.3	71.4	85.7	78.6	73.3	73.3	66.7	73.3	68.8	62.5
HcModLI	46.2	50.0	50.0	45.5	45.5	54.6	50.0	54.6	54.6	50.0
HcLapC	18	16	17	16	17	15	14	15	17	18
HcSC	11	12	12	11	12	12	12	12	11	12
HcSI	4.8	6.1	4.6	4.8	5.5	5.3	4.7	4.8	5.0	4.1
SL	6.0	4.0	4..0	4.0	4.0	4.0	4.0	4.0	4.0	3.0
SLI	37.5	28.6	28.6	28.6	26.7	26.7	20.0	26.7	25.0	25.0

7–20 mm ML (NMNZ M.287494) 37° 51′ 0″ S, 178° 35′ 0″ E, 20 m, 10/01/1980–11/01/1980, RV *James Cook*, Stn J01/15/80; 1♂, 11 mm ML (NMNZ M.067904) 37° 51′ 41″ S, 178° 54′ 42″ E, 30 m over 800 m, 11/01/1980, RV *James Cook*, Stn J01/17/80; 2♂, 7–14 mm ML, 1♀, 8 mm ML (NMNZ M.067314) 37° 51′ 42″ S, 178° 29′ 48″ E, 29–30 m, 10/01/1980, RV *James Cook*, Stn J01/14/80; 1♂, 14 mm ML (NMNZ M.067842) 37° 51′ 49″ S, 178° 29′ 49″ E, 30 m, 29/09/1979, RV *James Cook*, Stn J13/01/79; 8♂, 8–14 mm ML (NMNZ M.067838) 37° 52′ 03″ S, 178° 33′ 38″ E, 30 m, 29/09/1979, RV *James Cook*, Stn J13/02/79; 2♀, 15–17 mm ML (NMNZ M.287410) 38° 15′ 12″ S, 178° 38′ 36″ E, 139 m, 16/01/1979, RV *Tangaroa*, Stn 1979673; 1♂, 12 mm ML (NMNZ M.067846) 38° 22′ 09″ S, 178° 25′ 36″ E, 30 m, 30/09/1979, RV *James Cook*, Stn J13/07/79; 1♀, 9 mm ML (NMNZ M.016866) 38° 22′ 30″ S, 178° 40′ 0″ E, 161 m, 06/04/1963, RV *Ikatere*, Stn 1963044; 1♂, 13 mm ML, 3♀, 11–12 mm ML (NMNZ M.102124) 38° 41′ 30″ S, 174° 4′ 30″ E, 82–83 m, 18/08/1985, RV *Kaiyo Maru*, Stn KM/201A/85; 1♂, 13 mm ML, 2♀, 10–17 mm ML (NMNZ M.102128) 38° 48′ 18″ S, 172° 57′ 18″ E, 120 m over 146 m, 22/08/1985, RV *Kaiyo Maru*, Stn KM/202B/85; 2♂, 14–17 mm ML, 2♀, 19–22 mm ML (NMNZ M.287430) 38° 48′ 48″ S, 173° 29′ 36″ E, 146 m, 09/01/1981, RV *Tangaroa*,

Table 3 *Sepioloidea jaelae* sp. nov. type series ♀ specimen counts and measurements

Collection Reg. no. Sex Type	NMNZ M.330526 ♀ Paratype	NMNZ M.330526 ♀ Paratype	NMNZ M.330526 ♀ Paratype	NMNZ M.330525 ♀ Paratype	NMNZ M.330525 ♀ Paratype	NMNZ M.330525 ♀ Paratype	NMNZ M.330526 ♀ Paratype	NMNZ M.330525 ♀ Paratype	NMNZ M.330525 ♀ Paratype	NMNZ M.330526 ♀ Paratype
ML	12.0	16.0	17.0	19.0	20.0	20.0	20.0	21.0	22.0	22.0
MWI	100.0	81.3	82.4	79.0	85.0	75.0	75.0	66.7	68.2	72.7
FWI	41.7	25.0	23.5	31.6	30.0	25.0	25.0	23.8	27.3	22.7
FIIa	33.3	25.0	17.7	31.6	25.0	20.0	25.0	23.8	22.7	18.2
FII	66.7	50.0	47.1	42.1	55.0	50.0	50.0	47.6	50.0	50.0
FuLI	83.3	68.8	58.8	63.2	60.0	55.0	55.0	47.6	45.5	50.0
FFuI	33.3	25.0	23.5	26.3	30.0	20.0	25.0	14.3	18.2	18.2
HLI	75.0	50.0	58.8	63.2	55.0	50.0	55.0	52.4	50.0	45.5
HWI	100.0	68.8	70.6	68.4	45.0	80.0	60.0	66.7	63.6	63.6
EDI	25.0	12.5	17.7	15.8	15.0	15.0	15.0	14.3	13.6	13.6
OBWI	52.5	37.0	44.4	46.0	43.8	38.2	47.2	42.3	33.9	44.7
AL1I	83.3	56.3	47.1	57.9	55.0	60.0	50.0	57.1	54.6	50.0
AL2I	83.3	56.3	52.9	63.2	60.0	55.0	50.0	57.1	50.0	50.0
AL3I	91.7	62.5	52.9	63.2	60.0	65.0	60.0	57.1	54.6	50.0
AL4I	83.3	62.5	52.9	63.2	65.0	60.0	60.0	57.1	50.0	50.0
ASIn1	4.3	2.9	3.1	3.5	2.4	2.8	2.7	2.5	2.77	2.7
ASIn2	4.1	3.4	3.4	3.2	2.8	3.0	2.9	2.9	2.9	2.6
ASIn3	4.3	3.5	3.3	4.0	2.5	3.4	3.0	2.8	3.0	2.7
ASIn4	4.2	3.3	3.2	3.6	2.5	2.9	2.9	2.9	2.6	2.8
ASC1	39	38	35	42	40	42	36	45	42	41
ASC2	42	38	41	42	41	44	40	45	40	43
ASC3	44	39	38	41	43	44	41	48	44	49
ASC4	44	41	44	46	36	44	42	49	46	46
ClLI	33.3	25.0	23.5	26.3	20.0	25.0	20.0	23.8	22.7	18.2
ClRC	7	6	6	7	7	6	7	7	7	6
TIRC	31	34	28	35	30	37	32	32	32	38
ClSI	1.3	1.1	0.9	0.8	0.8	1.1	1.2	1.1	1.1	1.1
EgD	-	2.0	-	2.0	3.0	3.0	2.0	3.0	3.0	3.0
EgDI	-	12.5	-	10.5	15.0	15.0	10.0	14.3	13.6	13.6

Stn 1981791; 1♂, 14 mm ML, 3♀, 12–14 mm ML (NMNZ M.067831) 38° 50′ 04″ S, 178° 8′ 56″ E, 30–45 m, 02/10/1979, RV *James Cook*, Stn J13/23/79; 1♂, 11 mm ML, 1♀, 10 mm ML (NMNZ M.067841) 39° 31′ 0″ S, 172° 33′ 10″ E, 60 m over 190 m, 13/04/1980, RV *James Cook*, Stn J07/62/80; 4♂, 8–11 mm ML, 3♀, 8–16 mm ML, 1 indet., 11 mm ML (NMNZ M.067848) 39° 34′ 26″ S, 172° 35′ 04″ E, 127 m, 13/04/1980, RV *James Cook*, Stn J07/63/80; 1♀, 10 mm ML (NMNZ M.016862) 39° 40′ 30″ S, 177° 35′ 0″ E, 137–143 m, 07/04/1963, RV *Ikatere*, Stn 1963048; 4♂, 12–19 mm ML, 13♀, 10–19 mm ML (NMNZ M.067271) 39° 55′ 16″ S, 172° 29′ 51″ E, 133–207 m, 13/12/1978, RV *James Cook*, Stn J19/24/78; 4♀, 17–20 mm ML (NMNZ M.067896) 40° 4′ 35″ S, 172° 57′ 35″ E, 30 m, 13/10/1979, RV *James Cook*, Stn J14/09/79; 10♀, 18–20 mm ML (NMNZ M.067882) 40° 12′ 21″ S, 173° 1′ 42″ E, 80 m over 92 m, 13/10/1979, RV *James Cook*, Stn J14/10/79; > 30 specimens comprising both sexes, 14–16 mm ML (NMNZ M.330528) 40° 14′ 24″ S, 174° 0.1′ E, 96–101 m, 20/02/1983, RV *Kaharoa*; 3 indet., 8–9 mm ML (NMNZ M.102222) 40° 22′ 24″ S, 174° 23′ 12″ E, 111–112 m, 17/07/1985, RV *Kaiyo Maru*, Stn KM/104A/85; 3♂, 12–15 mm ML (NMNZ M.287500) 40° 23′ 48″ S, 173° 12′ 12″ E, 70–73 m, 02/05/1981, RV *James Cook*, Stn J07/04/81; 1♀, 16 mm ML (NMNZ M.074125) 40° 24′ 0″ S, 174° 17′ 0″ E, 110 m, 04/03/1976, RV *Acheron*, Stn 1976508; 1♀, 18 mm ML (NMNZ M.074123) 40° 30′ 30″ S, 174° 53′ 30″ E, 101 m, 01/03/1976, RV *Acheron*, Stn 1976484; 3♂, 6–16 mm ML, 2♀, 19–20 mm ML (NMNZ M.067883) 40° 31′ 24″ S, 173° 23′ 54″ E, 45 m, 14/10/1979, RV *James Cook*, Stn J14/14/79; 1♂, 9 mm ML, 1 indet., 8 mm ML (NMNZ M.074120) 40° 33′ 0″ S, 174° 7′ 0″ E, 132 m, 04/03/1976, RV *Acheron*, Stn 1976509; 1♂, 12 mm ML (NMNZ M.287427) 40° 34′ 30″ S, 172° 26′ 12″ E, 51–63 m over 53–64 m, 07/05/1981, RV *James Cook*, Stn J07/60/81; 1♂, 12 mm ML (NMNZ M.067890) 40° 35′ 33″ S, 171° 46′ 54″ E, 60 m over 182 m, 12/10/1979, RV *James Cook*, Stn J14/02/79; 5♂, 11–12 mm ML, 6♀, 16–19 mm ML (NMNZ M.074127); 1♂, 9 mm ML, 5♀, 14–17 mm ML (NMNZ M.287429): 40° 38′ 30″ S, 174° 1′ 0″ E, 183–187 m, 04/03/1976, RV *Acheron*, Stn 1976510; 2♂, 12–13 mm ML (NMNZ M.067897) 40° 45′ 15″ S, 171° 40′ 12″ E, 10 m, 12/10/1979, RV *James Cook*, Stn J14/04/79; 1♀, 18 mm ML (NMNZ M.010933) 40° 48′ 0″ S, 174° 11′ 0″ E, 71 m, 03/01/1957, MV *Alert*, Stn 1957196; 1♂, 11 mm ML, 2♀, 16–17 mm ML (NMNZ M.067315) 40° 50′ 21″ S, 176° 20′ 18″ E, 130 m, 13/01/1980, RV *James Cook*, Stn J01/60/80; 2♀, 11–17 mm ML (NMNZ M.287408); 2♂, 12–13 mm ML, 2♀, 9–20 mm ML (NMNZ M.287409): 40° 54′ 24″ S, 176° 16′ 12″ E, 52 m, 25/04/1980, RV *James Cook*, Stn J08/85/80; 1♀, 22 mm ML (NMNZ M.067891) 40° 55′ 36″ S, 172° 1′ 12″ E, 30 m, 13/10/1979, RV *James Cook*, Stn J14/05/79; 2♀, 14–15 mm ML (NMNZ M.074119) 40° 57′ 30″ S, 174° 18′ 0″ E, 139–144 m, 03/03/1976, RV *Acheron*, Stn 1976500; 2♂, 16–17 mm ML, 2♀, 20–23 mm ML (NMNZ M.067875) 40° 58′ 18″ S, 172° 0′ 48″ E, 60 m, 13/10/1979, RV *James Cook*, Stn J14/06/79; 1♂, 11 mm ML, 1♀ 11 mm ML (NMNZ M.102257) 40° 59′ 30″ S, 170° 52′ 54″ E, 440 m over 500 m, 22/07/1985, RV *Kaiyo Maru*, Stn KM/105B/85; 2♂, 12–13 mm ML, 1♀, 10 mm ML (NMNZ M.021303) 41° 5′ 0″ S, 174° 10′ 58″ E, 10/05/1967, Coll. M. van Dooren; 1♂, 13 mm ML (NMNZ M.287508) 41° 10′ 0″ S, 177° 43′ 0″ E, 37 m over 53 m, 21/10/1969, RV *James Cook*, Stn J06/125/69; 1♀, 15 mm ML (NMNZ M.074091) 41° 14′ 48″ S, 174° 51′ 30″ E, 15 m, 16/01/1956, Stn VUZ32; 2♂, 9–11 mm ML, 2♀, 8–12 mm ML, 2 indet., 7–10 mm ML (NMNZ M.074097) 41° 16′ 42″ S, 174° 54′ 06″ E, 15–17 m, 20/01/1956, Stn VUZ47; 1♂, 8 mm ML, 1♀, 12 mm ML (NMNZ M.074095) 41° 18′ 24″ S, 174° 52′ 18″ E, 4–7 m, 18/01/1956, Stn VUZ40; 1♂, 12 mm ML, 1♀, 18 mm ML (NMNZ M.074096) 41° 18′ 24″ S, 174° 48′ 24″ E, 15–18 m, 18/01/1956, Stn VUZ38; 1♀, 17 mm ML (NMNZ M.067285) 41° 22′ 24″ S, 174° 46′ 54″ E, 30 m, 20/04/1979, RV *James Cook*, Stn J05/11/79; 1♀, 17 mm ML (NMNZ M.012962) 41° 40′ 0″ S, 174° 18′ 0″ E, 73 m, 05/12/1956, Coll. F. Abernethy, Stn 1956030; 8♂, 11–14 mm ML, 2♀, 12–13 mm ML (NMNZ M.067888) 41° 59′ 03″ S, 174° 18′ 48″ E, 57 m over 164 m, 16/12/1978, RV *James Cook*, Stn J19/36/78; 1 indet. (NIWA 121888*) 42° 15′ 40″ S, 170° 44′ 29″ E, 213–221 m, 13/08/2017, RV *Tangaroa*, Stn 1609/41; 1♂, 14 mm ML, 4♀, 15–19 mm ML (NMNZ M.067884) 42° 23′ 14″ S, 170° 43′ 05″ E, 158 m over 216–224 m, 10/12/1978, RV *James Cook*, Stn J19/05/78; 4 indet. (NIWA 157614*) 43° 4′ 25″ S, 175° 1′ 0″ E, 357–367 m, 14/08/2015, RV *Tangaroa*, Stn 1511/71; 4♂, 9–10 mm ML, 2♀, 8–9 mm ML (NMNZ M.287513) 43° 6′ 06″ S, 175° 20′ 30″ E, 153 m, 12/01/1979, RV *Tangaroa*, Stn 1979656; 1♀, 9 mm ML (NMNZ M.074093) 43° 9′ 0″ S, 175° 30′ 30″ E, 112 m, 23/01/1954, MV *Alert*, Stn 1954002; 6♂, 9–13 mm ML, 2♀, 12–13 mm ML (NMNZ M.091663) 43° 17′ 48″ S, 173° 23′ 12″ E, 65 m over 78–86 m, 16/08/1985, RV *Kaiyo Maru*, Stn KM/119C/85; 5 indet. (NIWA 157615*) 43° 27′ 4″ S, 169° 36′ 32″ E, 45–48 m, 12/04/2019, RV *Kaharoa*, Stn KAH1902/69; 1 indet. (NIWA 95247*) 43° 30′ 0″ S, 177° 18′ 0″ W, 170–187 m, 27/10/2020, SOP TRIP4567/80; 1♂, 12 mm ML, 2♀, 16–17 mm ML (NMNZ M.067269) 43° 50′ 35″ S, 174° 42′ 10″ E, 400 m, 01/06/1979, RV *James Cook*, Stn J07/01/79; 3♂, 12–13 mm ML, 4♀, 12–18 mm ML (NIWA 142310) 44° 0′ 29″ S, 173° 38′ 35″ E, 123 m, 30/10/1979, Coll. NZOI, Stn S176; 3♂, 13–14 mm ML, 5♀, 12–21 mm ML (NMNZ M.091662) 44° 51′ 54″ S, 171° 33′ 0″ E, 40–46 m over 67–69 m, 12/08/1985, RV *Kaiyo Maru*, Stn KM/116A/85; 6♂, 16–17 mm ML, 2♀, 23–24 mm ML (NMNZ M.013473) 45° 7′ 30″ S, 171° 10′ 36″ E, 44–55 m, 11/1960, Coll. J. Graham; 2♂, 9–14 mm ML, 1♀, 8 mm ML (NMNZ M.102260) 47° 53′ 06″ S, 166° 57′ 0″ E, 120–151 m over 120–153 m, 01/08/1985, RV *Kaiyo Maru*, Stn KM/113A/85; 1♀, 19 mm ML (NIWA 95127) 49° 12′ S, 167° 18′ E, 90 m, 21/03/2015, Coll. SOP; 3♂, 11–12 mm ML (NMNZ M.102261) 48° 30′ 12″ S, 167° 0′ 42″ E, 50–110 m over 142–144 m, 02/08/1985, RV *Kaiyo Maru*, Stn KM/113B/85; 1 indet. (NIWA 157617*) 50° 30′ 0″ S, 167° 18′ 0″ E, 160–228 m, 15/04/2016, Stn 466923.

Etymology: The specific name was chosen in honour of the first author's mother, Jael Santos.

Diagnosis: Mantle length up to ~ 19 mm in mature males and ~ 24 mm in mature females. Anterior mantle margin without fringing projections. All arm suckers biserial throughout. Male and female arm suckers uniformly decrease in size from base to distal tip. Females often with thick, ruffled buccal membrane visible ventrally between Arms IV. Ventral left arm hectocotylised; distal ~ 50% of arm modified; basal unmodified section with ~ 6 sucker pairs. Modified section of hectocotylus slightly curved, without suckers but with sucker pedicels joined basally and modified forming ~ 16 lappets; each lappet consists of two laterally positioned spire-like projections with globular tips, decreasing in size to distal tip of arm. Tentacular club suckers in transverse rows of approximately seven; suckers small and uniform in size. Chromatophores mostly small and dot-like; dorsal often with larger, pale, irregular-shaped spots; no stripes.

Description: Mature males generally smaller than mature females: ML mature males 14.0–*15.0*–16.0 mm (SD 0.8), mature females 12.0–*18.9*–22.0 mm (SD 3.1). Mantle short, broad; maximum length and width subequal; posterior margin rounded (Fig. 4a–d); MWI males 73.3–*83.4*–93.3 (SD 6.1), females 66.7–*78.5*–100.0 (SD 9.6). Fins small, narrow; FWI males 18.8–*22.0*–31.3 (SD 4.3), females

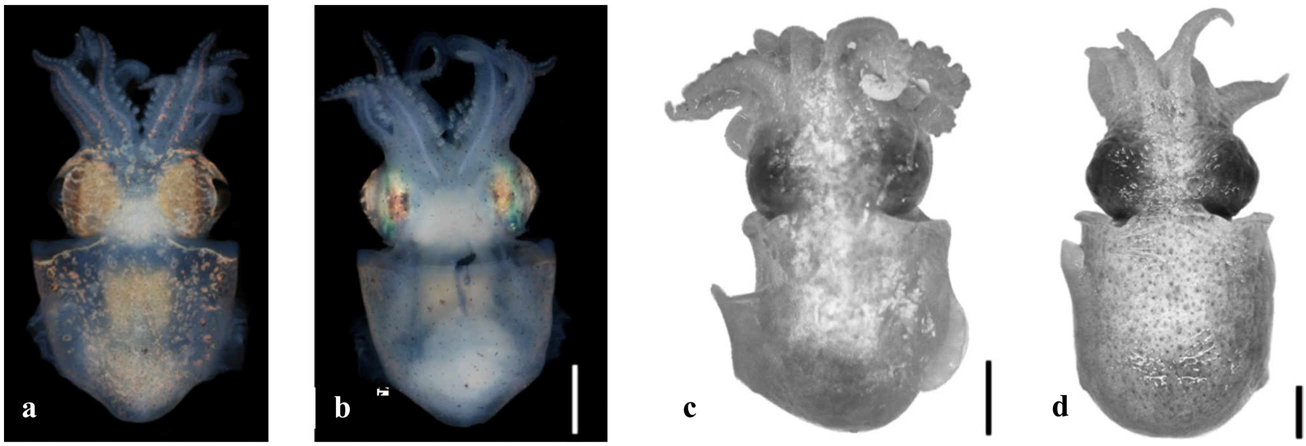

Fig. 4 *Sepioloidea jaelae* sp. nov.: **a** specimen photographed shortly after capture, dorsal view, ♂, 13 mm ML, NIWA 55378; **b** ventral view, same specimen (photos: Rob Stewart, NIWA, Oceans Survey from 20/20 Bay of Islands Survey); **c** holotype dorsal view, NMNZ M.287489, ♂, 16 mm ML; **d** paratype, dorsal view, NMNZ M.330525, ♀, 20 mm ML. Scale bars 5 mm

22.7–*27.6*–41.7 (SD 5.7). Fin length approximately 45% ML; FII males 31.3–*40.7*–50.0 (SD 5.7), females 42.1–*50.8*–66.7 (SD 6.4). Fins positioned towards posterior end of mantle; FIIa males 25.0–*28.8*–40.0 (SD 5.1), females 17.6–*24.2*–33.3 (SD 5.2); anterior fin margin does not reach anterior mantle margin. Anterior margin of fin convex often with lobes projecting slightly beyond anterior junction with mantle. Posterior fin tapers to its posterior junction with the mantle.

Head wider than long in both sexes: HLI males 50.0–*60.2*–66.7 (SD 5.4), females 45.5–*55.5*–75.0 (SD 8.5); HWI males 68.8–*76.1*–92.9 (SD 8.1), females 45.0–*68.7*–100.0 (SD 14.2). Occipital band width approximately 25% mantle length in both sexes; OBWI males 18.8–*26.8*–37.5 (SD 6.5); females 20.0–*24.5*–30.0 (SD 3.4). Two pores present on each side of head: one posterolateral to eye, one anteroventral to eye. Eyes large in both sexes, occupying significant portion of head; aperture covered by transparent membrane; EDI males 14.3–*19.3*–25.0 (SD 3.2), females 12.5–*15.7*–25.0 (SD 3.5).

Funnel long; FuLI males 50.0–*54.1*–64.3 (SD 4.9), females 45.5–*58.7*–83.3 (SD 11.2); muscular; broad basally, tapering to nearly cylindrical anteriorly. Funnel aperture located approximately at level of anterior margin of eye; FFuI males 18.8–*22.1*–28.6 (SD 3.8), females 14.3–*23.4*–33.3 (SD 5.8). Funnel valve small, semi-circular flap inside dorsal rim of funnel aperture. Funnel organ (Fig. 5a) with broad, rounded, wedge-shaped ventral components, broadest anteriorly; dorsal component roughly diamond-shaped in outline, apex almost meeting ventral component; anterior margin, with small protrusion.

Funnel component of funnel-mantle locking cartilage (Fig. 5b, c) comprised of two parts: a deep, ovular anterior pocket (concavity deepest posteriorly) and shallower narrow posterior groove. Mantle component (Fig. 5d) complements funnel component; anterior lobe prominent and nose-like in shape; posterior protuberance a narrow ridge.

Arms (Fig. 5e, f) broad basally, tapered distally; more robust in females than in males. Arm formula variable; typically, as follows: males, IV > III = II > I; females, III > IV > II = I; ALI4 males 71.4–*75.4*–85.7 (SD 4.1), ALI3 females 50.0–*61.7*–91.7 (SD 11.6), ALI1 males 62.5–*68.7*–75.0 (SD 4.0), females 47.1–*57.1*–83.3 (SD 10.1). All arms similar in shape, subtriangular in cross-section along whole arm. Arm suckers biserial throughout; suckers spherical with chitinous rims. Arms connected by membranous web, shallowest between Arms I (~ 10% arm length), deepest between Arms IV (~ 20% arm length); depths similar in both sexes. Females often with thick, ruffled buccal membrane (Fig. 5f) visible ventrally between Arms IV.

Arm-sucker counts and sizes differ between sexes with males having fewer but larger arm suckers; ASC1–4 males 24–*29*–32 (SD 2.6), 24–*28*–31 (SD 2.4), 26–*32*–38 (SD 3.2), 24–*31*–35 (SD 3.4), respectively; females 35–*40*–45 (SD 3.1), 38–*42*–45 (SD 2.1), 38–*43*–49 (SD 3.5), 41–*45*–49 (SD 2.4), respectively. Sucker size pattern similar in males and females; largest basally, tapering gradually to tip of arm without markedly enlarged suckers. Male suckers relatively larger than those of females; distinctly globular in shape; not embedded in arm or with surrounding tissue. Female suckers often inset within arm with protective membrane bordering lateral sucker margins. Sucker diameter larger in males than females; ASIn1–4 and HcSI males 4.3–*4.8*–5.4 (SD 0.4), 4.6–*5.2*–6.1 (SD 0.5), 4.8–*5.5*–6.0 (SD 0.5), 4.4–*5.3*–6.1 (SD 0.5), 4.1–*5.0*–6.1 (SD 0.5), respectively; ASIn1–4 females 2.4–*3.0*–4.3 (SD 0.6), 2.6–*3.1*–4.1 (SD 0.4), 2.5–*3.2*–4.3 (SD 0.6), 2.5–*3.1*–4.2 (SD 0.5), respectively.

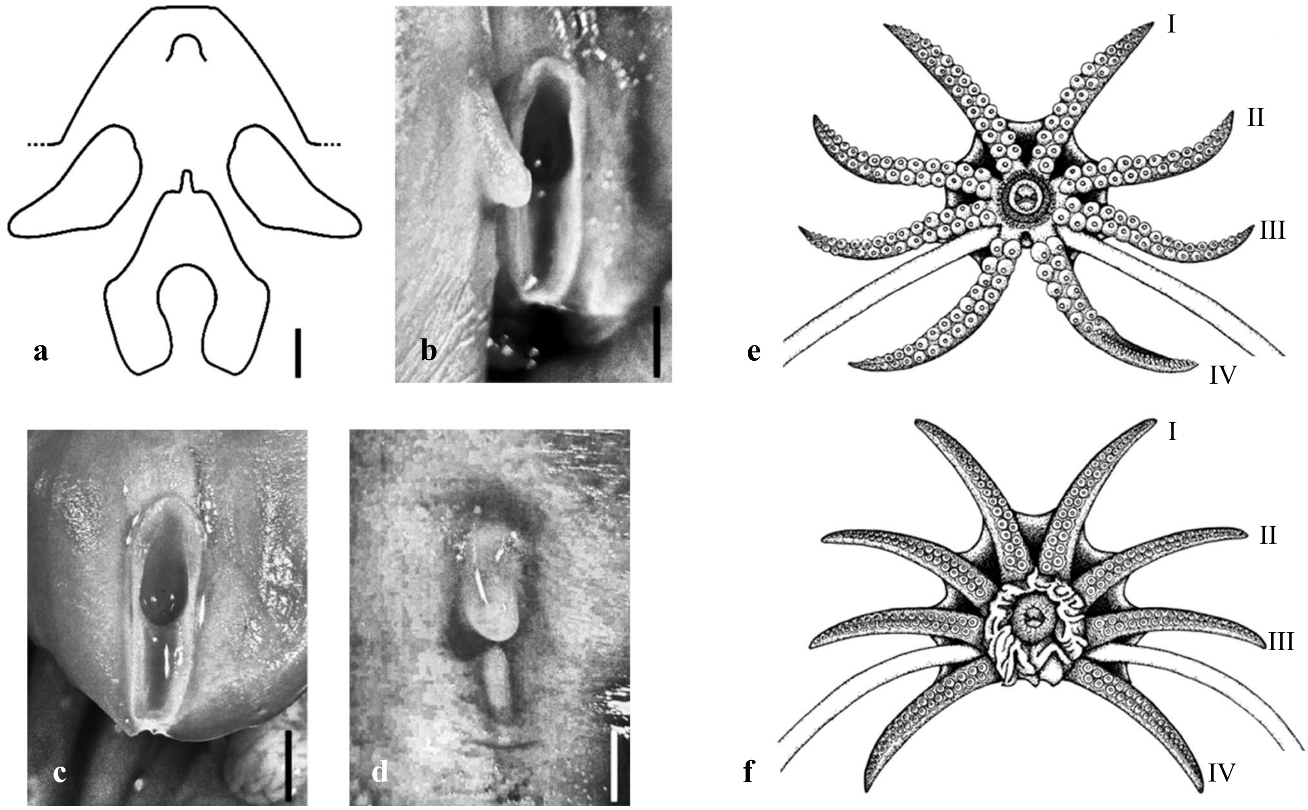

Fig. 5 *Sepioloidea jaelae* sp. nov.: **a** funnel organ schematic based on NMNZ M.067882, ♀, 20 mm ML; **b** right locking cartilage, mantle component, lateral view and funnel component, ventral view, NMNZ M.330525, ♀ paratype, 20 mm ML; **c** right locking cartilage, funnel component, NMNZ M.330525, ♀ paratype, 20 mm ML; **d** right locking cartilage, mantle component, NMNZ M.330525, ♀ paratype, 20 mm ML; **e** ♂ arm crown composite schematic based on type material with arms numbered I–IV; **f** ♀ arm crown composite schematic based on type material with arms numbered I–IV. Scale bars a, 2 mm; b–d, 1 mm

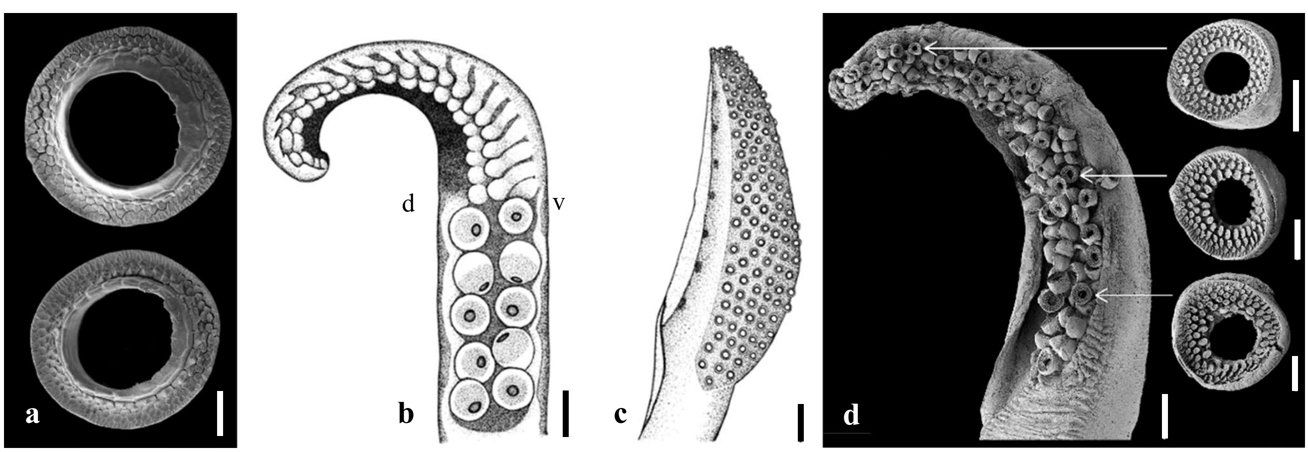

Fig. 6 *Sepioloidea jaelae* sp. nov.: **a** SEM images, upper, right Arm I sucker rim, NMNZ M.330528, ♂, 16 mm ML; lower, right Arm II sucker rim, NMNZ M.330528, ♀, 23 mm ML; **b** hectocotylised left Arm IV, oral view, NMNZ M.330528, ♂, 15 mm ML; **c** left tentacular club, NMNZ M.287502, ♂, 14 mm ML; **d** SEM images left tentacular club (left image) and club suckers (right images), NMNZ M.330528, ♀, 20 mm ML. Abbreviations: *d*, dorsal; *v*, ventral. Scale bars a, 50 µm; b, 1 mm; c, 300 µm; d, club 300 µm, suckers 50 µm

Arm-sucker rings without teeth (Fig. 6a). Infundibular ring slightly crenulated with ~ 16–23 raised blocks with flat inner margins and pointed outer margins. Papillated ring with 3 or 4 concentric rings of polygonal processes. Internal ring consists of ~ 15–20 pentagonal polygonal processes; inner margin flat, outer margin pointed; each process with

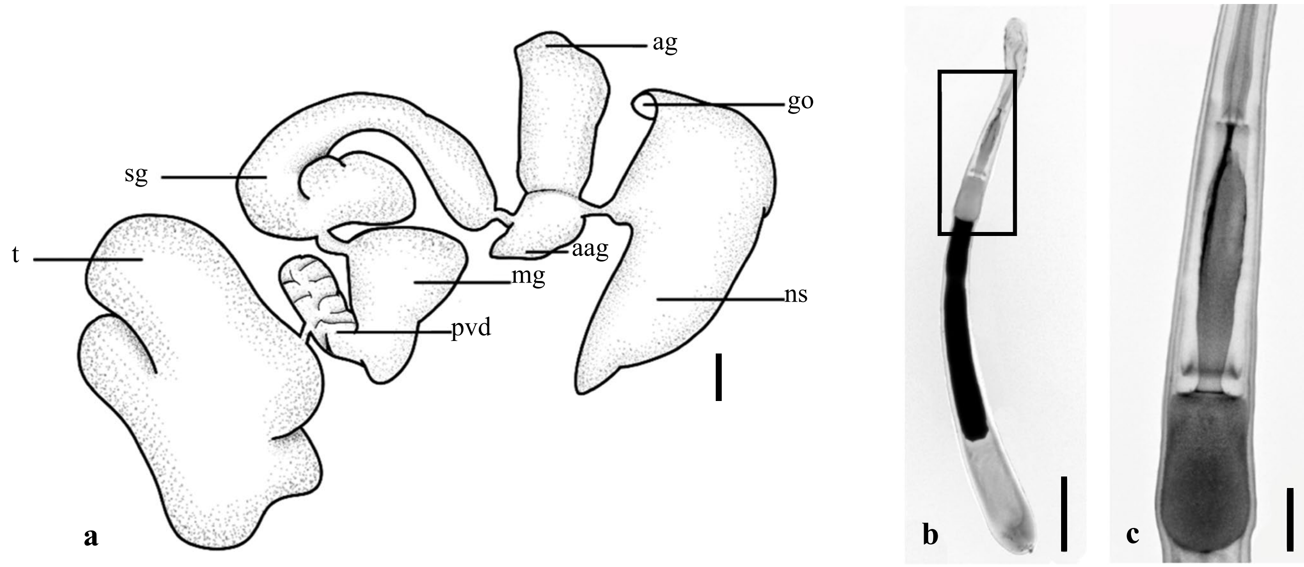

Fig. 7 *Sepioloidea jaelae* sp. nov.: **a** reproductive system, NMNZ M.330524, ♂ paratype, 14 mm ML; **b** whole spermatophore, cement body outlined, NMNZ M.330524, ♂ paratype, 31 mm ML; **c** enlargement of cement body, NMNZ M.330524, ♂ paratype, 31 mm ML. Abbreviations: *aag*, appendix of accessory gland; *ag*, accessory gland; *go*, genital opening; *mg*, mucilaginous gland; *ns*, Needham's sac; *pvd*, posterior vas deferens; *sg*, spermatophoric gland; *t*, testis. Scale bars a, 2 mm; b, 500 µm; c, 100 µm

subtle ridge-like peg running medially from inner to outer margins. Intermediate rings with ~ 55–90 flat, scale-like polygonal processes. External ring with slightly smaller and more numerous processes.

Left ventral arm of males hectocotylised (Fig. 6b); HcLI 62.5–*73.5*–85.7; unmodified proximal section with 5 or 6 normal sucker pairs; distal tip modified; HcMLI 45.5–*50.1*–54.5 (SD 3.6). Modified section devoid of suckers; modified sucker pedicel pairs form fused lappets; HcLPC 14.0–*16.0*–18.0 (SD 1.3). Each lappet comprised of two laterally positioned spire-like projections with globular tips, decreasing in size to distal tip of arm.

Tentacle stalks approximately 3–4 × mantle length, slender, oval in cross-section, without suckers. Clubs (Fig. 6c) expanded, tapering to blunt tips; ClLI males 20.0–*24.7*–28.6 (SD 3.6), females 18.2–*23.8*–33.3 (SD 4.2). Clubs with small, uniformly sized suckers set in transverse rows of about seven. Largest club sucker diameters similar in both sexes; ClSI males 0.8–*1.1*–1.4 (SD 0.2), females 0.8–*1.1*–1.3 (SD 0.2). Dorsal keel extends slightly beyond sucker-bearing face of club. Tentacular club (Fig. 6d) suckers with symmetrical papillated ring. Internal ring with ~ 10–13 pegs. Three to four intermediate rings present. External ring with ~ 40 pegs. Pegs irregular ovoid in shape; surface pitted. Internal surface of rim processes elongated and concave.

Gills with approximately 20 lamellae per demibranch.

Male reproductive system (Fig. 7a) with testis occupying approximately 50% of posterior mantle cavity. Spermatophore (Fig. 7b, c) cement body bipartite. Cement body posterior part barrel-shaped, with slight median constriction, connecting to sperm reservoir via a narrow duct. Cement body anterior part narrower than posterior part, cylindrical, approximately 150% length of posterior part, connecting to posterior part via narrow ridged 'neck'. Ejaculatory apparatus coiled, extending into anterior dilation of spermatophore. Spermatophore length approximately quarter of mantle length; SLI 20.0–*27.3*–37.5 (SD 4.4).

Eggs approximately spherical in shape; EgDI 10.0–*13.1*–15.0 ($n = 8$, SD 1.9).

Upper and lower beaks (Fig. 8a–c) transparent at posterior margin, darkening to brown then black towards beak tips. Lower beak (Fig. 8a, b) with beak height roughly equal to baseline length. Baseline length extends just beyond rostral tip. Hood length slightly more than half crest length; hood closely adherent to crest. Jaw angle obtuse. Wing length roughly two-thirds beak height. Wing width largest at jaw angle; marginally wider than minimum wing width. Lower rostral length roughly one-third of beak height. Upper beak (Fig. 8c) height roughly equal to beak length. Hood clear of crest posteriorly, with hood height around one-fifth of beak height. Upper rostral length over one-third crest length. Rostral tip pointed. Jaw angle almost 90°.

Radula (Fig. 8d) with rows of seven teeth. Rachidian teeth unicuspid, with long, narrow mesocone; base width approximately two-thirds mesocone height; proximal margin concave; underside with longitudinal indentation. First lateral teeth bicuspid with asymmetrical lateral margins; mesocone robust, its height about one-third rachidian teeth height, angled weakly towards rachidian teeth; inner margin concave from tip to base; outer cusp around two-thirds mesocone

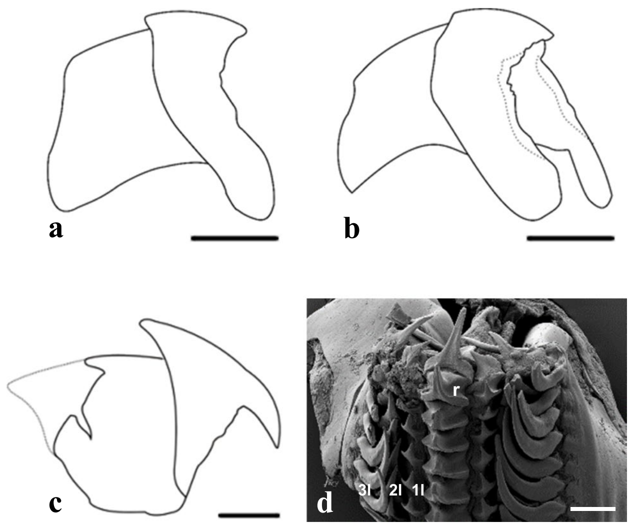

Fig. 8 *Sepioloidea jaelae* sp. nov.: **a** lower beak schematic, profile view, NMNZ M.95127, ♀, 19 mm ML; **b** lower beak schematic, oblique view, specimen as in a; **c** upper beak schematic, profile view, specimen as in a; **d** SEM image of radula, NMNZ M.330528, ♀, 20 mm ML. Abbreviations: r, rachidian tooth; 1 l, first lateral tooth; 2 l, second lateral tooth; 3 l, third lateral (or marginal) tooth. Scale bars a–c, 1 m; d, 100 µm

height. Second lateral teeth simple, unicuspid, approaching rachidian height, leaning weakly towards rachidian teeth. Marginal teeth simple, curved proximally, straight distally, longer than rachidian teeth.

Preserved specimen colouration varies from pale cream through to dark brown. Chromatophores (Fig. 3b) tiny dots and larger spots, dark brown/purple, evenly distributed across dorsal surface of the mantle, fins, head, and along Arms I, II, and III; fewer on ventral surfaces of the mantle, fins, head, and along Arms IV. Chromatophores present on aboral surface of tentacle club; small and densely set near tip, larger and very sparse proximally, extending along stalk for 150% club length.

Type locality: Southern Taranaki Basin, New Zealand, 40° 14′ 24″ S, 174° 0′ 6″ E, 96–101 m.

Distribution (Fig. 1c): Southwest Pacific, New Zealand; 0–440 m.

Remarks: At maturity, *S. jaelae* sp. nov. is unlikely to be mistaken for any other *Sepioloidea* species apart from *S. pacifica*. At all specimen sizes, it clearly differs from all other congeners (as summarised in Table 7) and additionally does not appear to reach sizes greater than ML 20 mm at maturity, further separating it from *S. magna* and *S. virgilioi* sp. nov. (maximum size for males ML ~ 45 v. ~ 37 mm, respectively; for females: ~ 62 v. ~ 59 mm ML). While the similar maximum sizes, overall morphological similarities, and geographic co-occurrence of *S. jaelae* sp. nov. and *S. pacifica* could potentially lead to confusion, these taxa can be reliably distinguished by differences in club morphology, and hectocotylus structure.

While the modified portion of the hectocotylus in both species spans the distal half of the arm length, the lappet structures are vastly different. In *S. jaelae* sp. nov., the dorsal and ventral lappet components are identical, globular, spire-like structures (Fig. 6b). However, in *S. pacifica*, the dorsal lappet component is asymmetrically bilobed (like the capital letter 'B') and the ventral lappet component is a simple flap (Fig. 2b).

Arm sucker and tentacle club sucker ring dentition also differs clearly between *S. jaelae* sp. nov. and *S. pacifica.* Arm suckers of both species have a papillated ring consisting of ~ 4 concentric rings with the internal ring consisting of medially ridged polygonal processes. In *S. pacifica*, these ridges continue in the intermediate ring of polygonal processes as straight or crescent-shaped pegs (Fig. 2a), the pegs are more prominent in females; pegs are absent in *S. jaelae* sp. nov. (Fig. 6a). The tentacular club suckers are arranged in transverse rows of around seven in *S. jaelae* sp. nov., compared to five in *S. pacifica.*

A large majority of female *S. jaelae* sp. nov. specimens also have a thick, ruffled buccal membrane around the entire oral aperture (Fig. 5f), usually thickest ventrally, often clearly visible in ventral view between Arms IV. All spermatangia observed in female specimens of *S. jaelae* sp. nov. in this study were embedded in the inner parts of this buccal area. This buccal membrane morphology was also occasionally observed in *S. pacifica* and *S. virgilioi* sp. nov.

In the published literature, there is only one potential instance of *S. jaelae* sp. nov. likely reported under the name *S. pacifica*. Reid (2009: 108) cited the depth range reported by Powell (1979: 440) for *S. pacifica* as 15–550 m. Observations made in the present study suggest that encountering *S. pacifica* in waters at the deeper end of this range is unlikely. All *S. pacifica* examined in this study were collected at depths not exceeding 55 m. It is probable that collection data for specimens previously misidentified as *S. pacifica*, but now recognised as *S. virgilioi* sp. nov. and/or *S. jaelae* sp. nov. were included in this estimated depth range.

Sepioloidea virgilioi sp. nov.

http://zoobank.org/A3189E62-0113-432D-810C-9E7D6BEDCB3D
(Figs 1, 3, 9–17; Tables 4, 5, 6 7 and 8).
Sepioloidea pacifica (Kirk, 1882): Dell (1959) (in part); Hurst (1969) (in part); Powell (1979) (in part).

Type material examined: New Zealand: *Holotype*: 1♂, 28 mm ML (NMNZ M.118323) 50° 40′ S, 167° 06′ E, 367–528 m, 02/1994, FV *Peterson*.

Paratypes: 5♂, 30–33 mm ML (NMNZ M.330520); 4♂, 26–30 mm ML (NMNZ M.330521); 4♀, 50–56 mm ML (NMNZ M.330522); 3♀, 40–55 mm ML (NMNZ M.330523): 50° 40′ S, 167° 06′ E, 367–528 m, 02/1994, FV *Peterson*; 1♀, 54 mm ML (NIWA 95297*) 50° 30′ S,

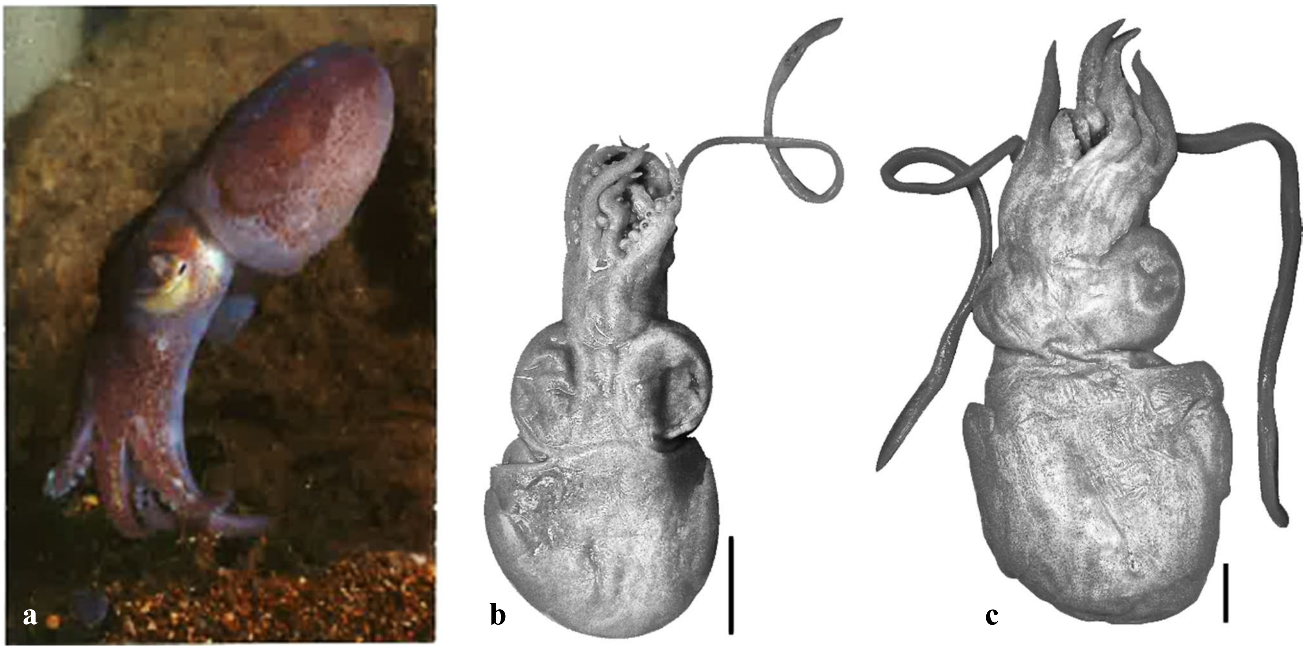

Fig. 9 *Sepioloidea virgilioi* sp. nov.: **a** live animal described as 'deep-water specimen' by Hurst (1969:9) thought to be *S. pacifica* but likely *S. virgilioi* sp. nov., 25–27 mm ML; **b** holotype, dorsal view, NMNZ M.118323, ♂, 28 mm ML; **c** paratype, dorsal view, NMNZ M.330522, ♀, 50 mm ML. Scale bars 10 mm

167° 18′ E, 160–228 m, 15/04/2016, SOP Trip 4669/23; 2♀, 36–47 mm ML (NIWA 128471*) 51° 2′ 31″ S, 167° 7′ 33″ E–51° 1′ 26″ S, 167° 9′ 7″ E, 492 m, 09/03/2007, Stn TON0701/55.

Other material examined: New Zealand: 1♀, 39 mm ML (NMNZ M.074144) 34° 49′ 0″ S, 174° 17′ 0″ E, 468–475 m, 24/02/1974, RV *Acheron*; 1♀, 49 mm ML (NMNZ M.015785) 35° 28′ 0″ S, 175° 19′ 0″ E, 512 m, 11/11/1962, RV *Ikatere*, Stn 1962075; 1♂, 29 mm ML (NMNZ M.015786^) 35° 28′ 0″ S, 175° 19′ 0″ E, 366 m, 28/09/1962, RV *Ikatere*; 1♀, 51 mm ML (NMNZ M.287476) 36° 35′ 22″ S, 176° 10′ 29″ E, 355 m, 08/01/1995, RV *Kaharoa*, Stn KAH9501/18; 1♂, 19 mm ML (NIWA 142285*) 36° 40′ 55″ S, 176° 14′ 46″ E, 470–468 m, 24/01/1998, Coll. NIWA, MFish on RV *Kaharoa*, Stn KAH9801/37; 1♀, 46 mm ML (NIWA 84776) 37° 0′ 25″ S, 176° 16′ 41″ E, 425 m, 21/10/1996, Coll. NIWA, MFish, Z8579; 1♀, 51 mm ML (NIWA 84774); 1♀ 46 mm ML (NIWA 84775): 37° 5′ 36″ S, 176° 15′ 12″ E, 393 m, 22/01/1998, Coll. MFish, NIWA, Z9011; 1♀, 22 mm ML (NIWA 142297*) 37° 8′ 38″ S, 176° 19′ 37″ E, 472–473 m, 21/01/1998, Coll. NIWA, MFish on RV *Kaharoa*, Stn KAH9801/23; 1♀, 26 mm ML, 1 indet., 15 mm ML (NIWA 142299*) 37° 25′ 12″ S, 176° 36′ 29″ E, 557–537 m, 19/01/1998, Coll. NIWA, MFish on RV *Kaharoa*, Stn KAH9801/13; 1♀, 47 mm ML (NMNZ M.118390) 37° 31′ 38″ S, 176° 37′ 1″ E, 310–345 m, 10/01/1994, RV *Kaharoa*, Stn KAH9401/25; 1♀, 51 mm ML (NIWA 84785) 37° 37′ 0″ S, 176° 48′ 30″ E, 360 m, 21/01/1998, Z9005; 1♂, 23 mm ML, 3♀, 27–35 mm ML (NIWA 84777) 41° 4′ 10″ S, 176° 21′ 47″ E, 309 m, 08/05/1999, Coll. NIWA, MFish, Z9827; 1♀, 38 mm ML (NMNZ M.012959) 41° 34′ 18″ S, 174° 43′ 18″ E, 274 m, 29/08/1957, FV *Admiral*, Stn 1957099; 1♀, 36 mm ML (NMNZ M.015782^) 41° 34′ 18″ S, 174° 43′ 18″ E, 373 m, 25/09/1962, RV *Ikatere*; 1♀, 34 mm ML (NMNZ M.074103) 42° 26′ 30″ S, 170° 36′ 30″ E, 366 m, 23/11/1970, RV *James Cook*, Stn J22/59/70; 17♀, 45–59 mm ML (NMNZ M.119118); 13♀, 47–54 mm ML (NMNZ M.119118/1); 13♀, 29–54 mm ML (NMNZ M.119118/2); 2♀, 52–53 mm ML (M.119118/4): 42° 54′ 0″ S, 176° 26′ 0″ E, 368–411 m, 27/12/1994–18/01/1995, Coll. M. Marinovich on FV *Petersen*; 2 indet. (NIWA 106127*) 42° 54′ 23″ S, 177° 26′ 35″ E, 406–409 m, 16/08/2015, RV *Tangaroa*, Stn 1511/95; 1 indet. (NIWA 92514*) 42° 55′ 14″ S, 174° 36′ 57″ E, 911 m, 25/01/2014, RV *Tangaroa*, Stn 1401/131; 4 indet. (NIWA 106088*) 43° 4′ 25″ S, 175° 1′ 0″ E, 357–367 m, 14/08/2015, RV *Tangaroa*, Stn 1511/71; 1♀, 32 mm ML (NIWA 105547*) 43° 6′ 0″ S, 174° 50′ 24″ E, 450–480 m, 22/01/2016, Coll. MPI, NIWA on RV *Tangaroa*, Stn TAN1601/98; 1 indet. (NIWA 126973*) 43° 8′ 48″ S, 175° 32′ 29″ E, 414–422 m, 28/01/2018, RV *Tangaroa*, Stn TAN1801/112; 1 indet., 29 mm ML (NIWA 105544*) 43° 12′ 36″ S, 175° 45′ 0″ E, 425–442 m, 25/01/2016, Coll. MPI, NIWA on RV *Tangaroa*, Stn TAN1601/112; 1 indet. (NIWA 92512*) 43° 15′ 3″ S, 174° 46′ 1″ E, 429 m, 25/01/2014, RV *Tangaroa*, Stn TAN1601/112; 1♀, 48 mm ML (NIWA 155092) 43° 16′ 34″

Table 4 *Sepioloidea virgilioi* sp. nov. type series ♂ specimen counts and measurements

Collection Reg. no. Sex Type	NMNZ M.118323 ♂ Holotype	NMNZ M.330521 ♂ Paratype	NMNZ M.330521 ♂ Paratype	NMNZ M.330520 ♂ Paratype	NMNZ M.330521 ♂ Paratype	NMNZ M.330521 ♂ Paratype	NMNZ M.330520 ♂ Paratype	NMNZ M.330520 ♂ Paratype	NMNZ M.330520 ♂ Paratype	NMNZ M.330520 ♂ Paratype
ML	28.0	26.0	29.0	30.0	30.0	30.0	31.0	33.0	33.0	33.0
MWI	121.4	107.7	96.6	96.7	103.3	96.7	93.5	97.0	90.9	72.7
FWI	21.4	-	24.1	20.0	13.3	13.3	19.4	18.2	21.2	27.3
FIIa	21.4	-	31.0	20.0	26.7	36.7	22.6	24.2	30.3	24.2
FII	53.6	-	58.6	46.7	50.0	50.0	61.3	48.5	45.5	54.5
FuLI	60.7	57.7	65.5	63.3	40.0	43.3	58.1	60.6	51.5	60.6
FFuI	21.4	26.9	31.0	30.0	16.7	26.7	16.1	27.3	18.2	33.3
HLI	100.0	92.3	79.3	70.0	86.7	86.7	87.1	66.7	72.7	81.8
HWI	100.0	100.0	86.2	83.3	83.3	63.3	87.1	93.9	93.9	87.9
EDI	21.4	26.9	20.7	20.0	16.7	20.0	25.8	24.2	18.2	21.2
OBWI	67.9	42.3	34.5	43.3	33.3	46.7	48.4	48.5	48.5	36.4
AL1I	82.1	65.4	58.6	66.7	53.3	66.7	80.6	75.8	63.6	69.7
AL2I	89.3	84.6	96.6	70.0	70.0	70.0	87.1	87.9	66.7	69.7
AL3I	107.1	76.9	96.6	90.0	70.0	70.0	83.9	81.8	75.8	87.9
AL4I	85.7	100.0	106.9	96.7	66.7	90.0	83.9	90.9	78.8	90.9
ASIn1	7.3	7.4	7.1	5.9	5.3	6.5	6.8	5.9	5.8	6.8
ASIn2	8.0	8.2	7.6	6.1	6.2	7.6	7.7	6.6	5.7	6.9
ASIn3	8.1	7.7	7.2	6.5	6.2	6.4	7.3	6.7	6.1	6.7
ASIn4	8.2	6.4	5.9	5.2	4.7	5.5	6.5	4.9	4.6	6.7
ASC1	48	48	37	47	41	43	40	45	50	46
ASC2	51	47	48	51	45	46	45	48	51	50
ASC3	55	45	53	49	48	50	39	54	54	52
ASC4	43	55	57	49	49	57	55	64	55	53
ClLI	42.9	38.5	-	40.0	36.7	33.3	54.8	42.4	42.4	45.5
ClRC	9	8	-	8	8	8	9	8	6	8
TIRC	50	40	-	40	35	40	40	40	50	50
ClSI	0.7	0.7	-	0.8	0.8	0.9	0.8	0.7	0.8	0.7
HcLI	92.9	84.6	93.1	80.0	63.3	76.7	87.1	87.9	60.6	72.7
HcModLI	34.6	22.7	22.2	20.8	26.3	30.4	25.9	27.6	30.0	33.3
HcLapC	15	15	13	15	14	14	16	14	15	15
HcSC	28.0	28.0	28.0	26.0	27.0	28.0	28.0	29.0	28.0	27.0
HcSI	5.75	4.81	5.17	4.47	4.13	4.33	5.48	4.12	4.45	6.73
SL	5.0	9.0	8.0	6.0	7.0	7.0	7.0	6.0	7.0	9.0
SLI	17.9	34.6	27.6	20.0	23.3	23.3	22.6	18.2	21.2	27.3

S, 177° 5′ 51″ E, 250–275 m, 27/01/2018, RV *Tangaroa*, Stn TAN1801/109; 2♀, 38–44 mm ML (NIWA 128493*) 43° 22′ 1″ S, 178° 54′ 58″ E, 400–404 m, 19/12/2015, Coll. NIWA on RV *Tangaroa*, Stn TAN1516/155; 1♂, 16 mm ML, 1♀, 22 mm ML (NIWA 106212*) 43° 22′ 12″ S, 178° 56′ 24″ E, 394–395 m, 20/08/2015, Coll. NIWA on RV *Tangaroa*, Stn TAN1511/134; 1 indet. (NIWA 131078*) 43° 25′ 44″ S, 177° 33′ 4″ E, 306 m, 06/06/2018, RV *Tangaroa*, Stn TAN1805/253; 1♀, 33 mm ML (NIWA 105547*) 43° 28′ 12″ S, 174° 45′ 36″ E, 349–372 m, 23/01/2016, Coll. MPI, NIWA on RV *Tangaroa*, Stn TAN1601/102; 1 indet. (NIWA 106078*) 43° 31′ 21″ S, 174° 34′ 53″ E, 487–491 m, 13/08/2015, RV *Tangaroa*, Stn TAN1511/56; 1 indet. (NIWA 106082*) 43° 31′ 43″ S, 174° 35′ 22″ E, 482–487 m, 13/08/2015, RV *Tangaroa*, Stn TAN1511/65; 1♀, 33 mm ML (NIWA 106067*) 43° 31′ 44″ S, 174° 34′ 28″ E, 497–500 m, 11/08/2015, RV *Tangaroa*, Stn TAN1511/48; 1 indet. (NIWA 106059*) 43° 32′ 23″ S, 174° 35′ 2″ E, 496 m, 11/08/2015, RV *Tangaroa*, Stn TAN1511/50; 1 indet. (NIWA 92513*) 43° 39′ 44″ S, 175° 27′ 46″ E, 304 m, 22/01/2014, RV *Tangaroa*, Stn TAN1401/116; 1♀, 23 mm ML (NIWA 106117*) 43° 48′ 16″ S, 176° 35′ 52″ E, 465 m, 15/08/2015, RV *Tangaroa*, Stn TAN1511/89; 2 indet. (NIWA 106070*) 43° 54′ 50″ S, 175° 55′ 36″ E, 528–544 m, 08/08/2015, RV

Table 5 *Sepioloidea virgilioi* sp. nov. type series ♀ specimen counts and measurements

Collection	NIWA	NMNZ	NIWA	NMNZ	NMNZ	NMNZ	NMNZ	NIWA	NMNZ	NMNZ
Reg. no.	128471	M.330523	128471	M.330522	M.330522	M.330522	M.330523	95297	M.330523	M.330522
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
Type	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
ML	36.0	40.0	47.0	48.0	50.0	52.0	54.0	54.0	55.0	56.0
MWI	108.3	105.0	97.9	89.6	76.0	76.9	96.3	87.0	87.3	66.1
FWI	27.8	30.0	34.0	25.0	20.0	17.3	22.2	24.1	29.1	21.4
FIIa	19.4	30.0	14.9	22.9	22.0	19.2	20.4	18.5	14.5	19.6
FII	61.1	65.0	59.6	60.4	56.0	46.2	61.1	61.1	60.0	53.6
FuLI	61.1	57.5	55.3	60.4	46.0	48.1	50.0	37.0	41.8	53.6
FFuI	27.8	30.0	19.1	22.9	30.0	19.2	16.7	16.7	20.0	21.4
HLI	77.8	77.5	72.3	79.2	74.0	80.8	79.6	81.5	69.1	67.9
HWI	83.3	87.5	83.0	83.3	70.0	69.2	68.5	70.4	80.0	58.9
EDI	19.4	22.5	17.0	20.8	16.0	13.5	13.0	14.8	16.4	14.3
OBWI	47.2	52.5	44.7	43.8	46.0	42.3	37.0	44.4	38.2	33.9
AL1I	69.4	65.0	61.7	62.5	64.0	53.8	63.0	70.4	74.5	48.2
AL2I	69.4	64.3	57.4	70.8	60.0	51.9	61.1	70.4	58.2	53.6
AL3I	80.6	87.5	72.3	79.2	76.0	57.7	68.5	77.8	70.9	64.3
AL4I	88.9	85.0	76.6	81.3	76.0	69.2	79.6	75.9	74.5	62.5
ASIn1	3.0	3.0	2.5	2.5	2.5	2.4	2.2	2.1	2.0	2.1
ASIn2	3.1	3.1	2.6	2.2	2.3	2.3	2.2	2.0	2.3	2.1
ASIn3	3.2	3.3	2.7	2.6	2.3	2.3	2.2	2.2	2.2	2.4
ASIn4	2.8	3.0	2.3	2.6	2.5	2.3	2.3	2.1	2.0	2.3
ASC1	65	61	59	64	56	64	62	60	64	60
ASC2	70	34	63	64	56	64	64	56	75	60
ASC3	72	80	69	66	66	67	72	65	75	69
ASC4	74	71	76	69	70	63	70	65	70	69
ClLI	47.2	47.5	38.3	41.7	38.0	26.9	37.0	35.2	36.4	30.4
ClRC	10	10	9	10	9	9	9	11	11	11
TIRC	56	53	60	50	56	55	52	57	53	55
ClSI	0.7	0.7	0.8	0.8	0.7	0.5	0.7	0.6	0.7	0.5
EgD	-	6.0	6.0	10	8.0	6.0	7.0	7.0	8.0	7.0
EgDI	-	15.0	12.8	20.8	16.0	11.5	13.0	13.0	14.5	12.5

Tangaroa, Stn TAN1511/29; 1♀, (NIWA 106244*) 44° 2′ 11″ S, 179° 2′ 44″ E, 305–316 m, 23/08/2015, RV *Tangaroa*, Stn TAN1511/164; 1♀, 33 mm ML (NIWA 128485*) 44° 5′ 49″ S, 174° 43′ 56″ E, 510–516 m, 11/12/2015, RV *Tangaroa*, Stn TAN1516/59; 1♂, 1♀, 28 mm ML (NIWA 106095*) 44° 11′ 1″ S, 175° 52′ 14″ E, 444 m, 15/08/2015, RV *Tangaroa*, Stn TAN1511/75; 3♀, 42–50 mm ML (NIWA 128489*) 44° 15′ 36″ S, 176° 13′ 44″ E, 357–331 m, 10/12/2015, RV *Tangaroa*, TAN1516/65; 1♀, 24 mm ML (NIWA 106104*) 44° 15′ 44″ S, 176° 13′ 8″ E, 315–328 m, 16/08/2015, RV *Tangaroa*, Stn TAN1511/87; 1♀, 37 mm ML (NMNZ M.011047) 45° 44′ 0″ S, 171° 2′ 0″ E, 137 m, 23/01/1957, MV *Alert*, Stn 1957202; 1♂, 24 mm ML, 9 indet., 6–14 mm ML (NMNZ M.008944) 45° 45′ 24″ S, 171° 5′ 0″ E, 549 m, 16/08/1955, MV *Alert*, Stn 1955190; 2♂, 20–26 mm ML, 4♀, 29–33 mm ML, 2 indet., 14–17 mm ML (NMNZ M.008959) 45° 47′ 0″ S, 171° 7′ 0″ E, 457–549 m, 16/08/1955, Stn 1955191; 2♂, 23–24 mm ML (NIWA 84771) 48° 54′ 26″ S, 169° 34′ 55″ E, 800 m, 26/04/1998, Z9203; ~260 specimens comprising both sexes, 20–43 mm ML (NMNZ M.330527); 14♂, 20–34 mm ML, 12♀, 37–43 mm ML (NMNZ M.118323/1): 50° 40′ 0″ S, 167° 06′ 0″ E, 367–528 m, 02/1994, FV *Peterson*; 1♀, 37 mm ML (NMNZ M.287613) 51° 7′ 36″ S, 166° 35′ 54″ E, 515 m, 22/04/1997, Coll. C. Morrish on FV *Venture K*, Stn 991/17; 1♀, 46 mm ML (NMNZ M.287770) FV *Drysdale*, Stn DRY9602/01; 2♂, 30–35 mm ML, 3♀, 40–55 mm ML (NIWA 84772); 1♂, 29 mm ML, 2♀, 37–41 mm ML (NIWA 84783).

Comparative *Sepioloidea magna* Reid, 2009 material examined: 1♂, 62 mm ML (AM C.593493) 17° 17′ 0″ S, 120° 12′ 0″ E, 304 m, 03/02/1984.

Etymology: The specific name was chosen in honour of the first author's father, Virgilio Santos.

Diagnosis: Mantle length up to ~ 37 mm in mature males and ~ 56 mm in mature females. Anterior mantle margin without fringing projections. All arm suckers biserial throughout. Median arm suckers of males enlarged, most prominently sucker pairs 4–8 (counting from proximal-most pair) on Arms I–III. Ventral left arm hectocotylised; distal ~ 25% of arm modified; basal unmodified section with ~ 14 sucker pairs. Modified section of hectocotylus without suckers but with sucker pedicels joined basally forming ~ 15 lappets; each lappet comprises a dorsal spire-shaped structure with globular tip and a ventral tongue-shaped flap with lobed apex; from proximal to distal end of modified portion of arm, tips of lappets become pointed, rather than rounded. Tentacular club suckers in transverse rows of approximately ten; suckers tiny and uniform in size. Chromatophores small and dot-like; no stripes or spots.

Description: Species sexually dimorphic at maturity. Males smaller than females: ML mature males 26.0–*30.3*–33.0 mm (SD 2.3), mature females 36.0–*49.2*–56.0 mm (SD 6.7). Mantle short, broad; maximum length and width subequal; posterior margin rounded (Fig. 9a–c); MWI males 72.7–*97.6*–121.4 (SD 12.4), females 66.1–*89.0*–108.3 (SD 13.4). Fins small, narrow; FWI males 13.3–*19.8*–27.3 ($n = 9$, SD 4.6), females 17.3–*25.1*–34.0 (SD 5.1). Fin length approximately 60% ML; FII males 45.5–*52.1*–61.3 ($n = 9$, SD 5.4), females 46.2–*58.4*–65.0 (SD 5.3). Fins positioned towards posterior end of mantle; FIIa males 20.0–*26.4*–36.7 ($n = 9$, SD 5.4), females 14.5–*20.2*–30.0 (SD 4.4); anterior fin margin does not reach anterior mantle margin. Anterior margin of fin convex often with larger lobes projecting slightly beyond anterior junction with mantle. Posterior fin tapers to its posterior junction with mantle, rarely with tiny convex lobe.

Head length and width proportions similar in both sexes: HLI males 66.7–*82.3*–100.0 (SD 10.4), females 67.9–*76.0*–81.5 (SD 4.9); HWI males 63.3–*87.9*–100.0 (SD 10.6), females 58.9–*75.4*–87.5 (SD 9.2). Occipital band width approximately 50% mantle length in both sexes; OBWI males 33.3–*45.0*–67.9 (SD 10.0), females 33.9–*43.0*–52.5 (SD 5.4). Two pores present on each side of head: one posterolateral to eye, one anteroventral to eye. Eyes large in both sexes, occupying significant portion of head; aperture covered by transparent membrane; EDI males 16.7–*21.5*–26.9 (SD 3.3), females 13.0–*16.8*–22.5 (SD 3.2).

Funnel long; FuLI males 40.0–*56.1*–65.5 (SD 8.5), females 37.0–*51.1*–61.1 (SD 8.0); muscular; broad basally, tapering to nearly cylindrical anteriorly. Funnel aperture located approximately at level of anterior margin of eye; FFuI males 16.1–*24.8*–33.3 (SD 6.2), females 16.7–*22.4*–30.0 (SD 5.1). Funnel valve small, semi-circular flap with extended apex inside dorsal rim of funnel aperture. Funnel organ (Fig. 10a) with broad, rounded, wedge-shaped ventral components, broadest medially; dorsal component triangular, apex almost meeting ventral component anterior margin.

Funnel component of funnel-mantle locking cartilage (Fig. 10b) comprised of two parts: a deep, ovular anterior pocket (concavity deepest posteriorly) and shallower narrow posterior groove. Mantle component (Fig. 10c) complements funnel component; anterior lobe prominent and nose-like in shape; posterior protuberance a narrow ridge.

Arms (Fig. 10d, e) broad basally, tapered distally; more robust in females than in males. Arm formula variable; typically, as follows: males, IV > III = II > I; females, IV > III = I > II; ALI4 males 66.7–*89.0*–106.9 (SD 11.3), females 62.5–*77.0*–88.9 (SD 7.5), ALI1 males 53.3–*68.3*–82.1 (SD 9.2), ALI2 females 51.9–*61.4*–70.8 ($n = 9$, SD 7.2). All arms similar in shape, subtriangular in cross-section along whole arm. Arm suckers biserial throughout; suckers spherical with chitinous rims. Arms connected by membranous web; in males, web depth varies, shallowest between Arms I (one-quarter arm length), deepest between Arms III (one-third arm length), absent between ventral arm in both sexes; in females web extends to approximately half of arm length on all arms. Females with protective membrane bordering lateral margins of arm suckers.

Arm sucker counts and sizes differ between sexes with males having fewer but larger arm suckers; ASC1–4 males 37–*45*–50 (SD 4.1), 45–*48*–51 (SD 2.4), 39–*50*–55 (SD 5.0), 43–*54*–64 (SD 5.7), respectively; females 56–*62*–65 (SD 2.8), 56–*64*–75 (SD 6.1), 65–*70*–80 (SD 4.7), 63–*70*–76 (SD 3.8), respectively. Male arm suckers noticeably enlarged about halfway along each arm length, most prominent in sucker pairs 4–8 on Arms I–III (Fig. 10d) often with sudden decrease in size around distal 25% of arms; Arms IV sucker enlargement similar but less pronounced. All female arm suckers similar in size; largest basally, tapering gradually to tip of arm; no markedly enlarged suckers (Fig. 10e). Sucker diameters more than double in diameter in males compared to females; ASIn1–4 and HcSI males 5.3–*6.5*–7.4 (SD 0.7), 5.7–*7.0*–8.2 (SD 0.9), 6.1–*6.9*–8.1 (SD 0.7), 4.6–*5.9*–8.2 (SD 1.1), 4.1–*5.0*–6.7 (SD 0.8), respectively; ASIn1–4 females 2.0–*2.4*–3.0 (SD 0.4), 2.0–*2.4*–3.1 (SD 0.4), 2.2–*2.6*–3.3 (SD 0.4), 2.0–*2.4*–3.0 (SD 0.3), respectively.

Arm-sucker rings without teeth (Fig. 11a). Arm-sucker infundibular rings slightly crenulated with ~ 35–50 raised blocks. Papillated ring with 6–9 concentric rings of polygonal processes. Internal ring with ~ 30–55 laterally elongated, mound-like polygonal processes. Intermediate rings with ~ 50–170 scale-like polygonal processes; becoming flatter, smaller, and greater in number towards external ring.

Left ventral arm of males hectocotylised (Fig. 11b, c); HcLI 60.6–*79.9*–93.1; unmodified proximal section with 14–15 normal sucker pairs; distal tip modified; HcMLI 20.0–*27.4*–34.6 (SD 4.7). Modified section devoid of

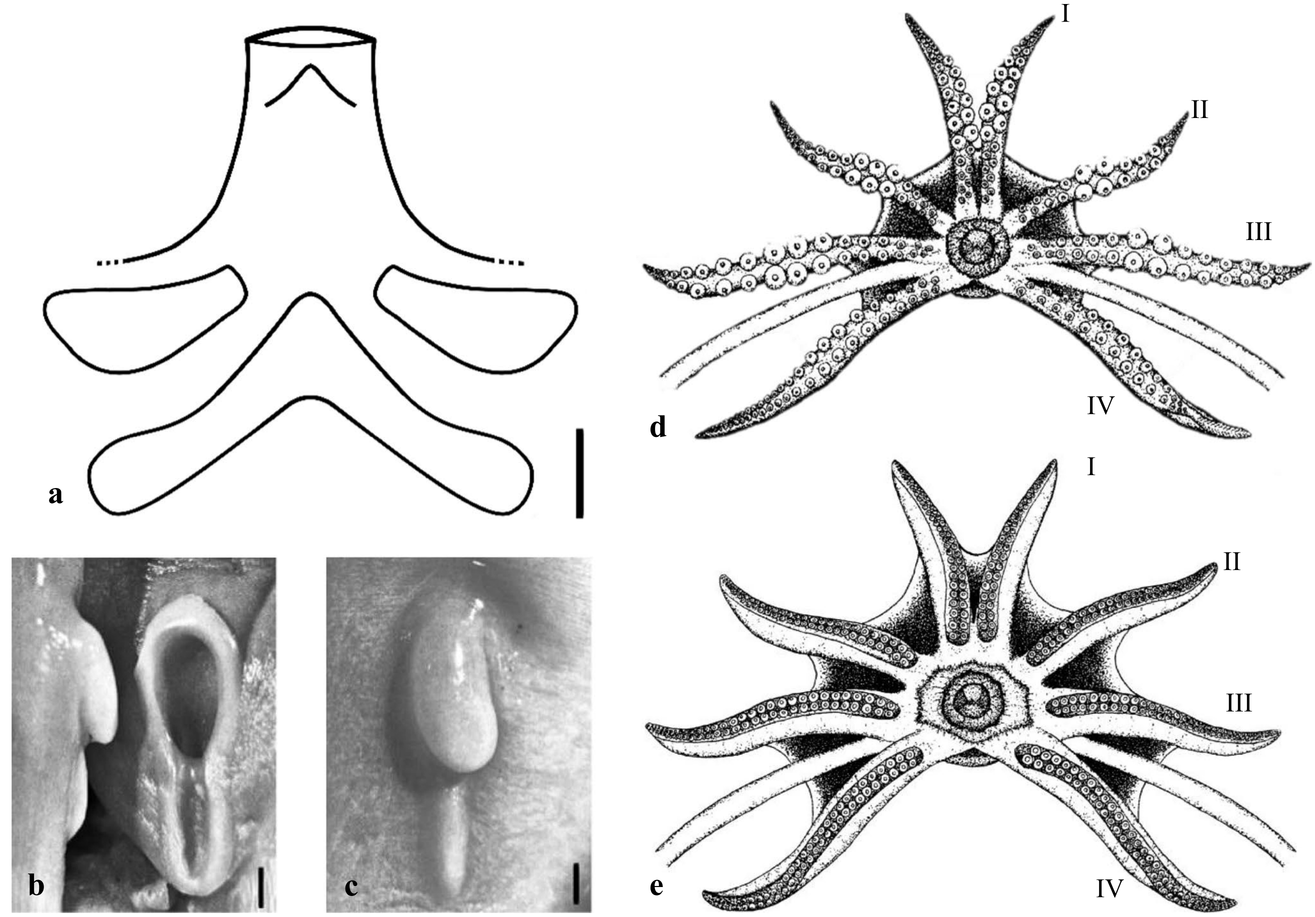

Fig. 10 *Sepioloidea virgilioi* sp. nov.: **a** funnel organ schematic based on NIWA 142281, ♀, 50 mm ML; **b** right locking cartilage, mantle component, lateral view and funnel component, ventral view, NMNZ M.330522, ♀ paratype, 48 mm ML; **c** right locking cartilage, mantle component, NMNZ M.330522, ♀ paratype, 48 mm ML; **d** ♂ arm crown composite schematic based on type material with arms numbered I–IV; **e** ♀ arm crown composite schematic based on type material with arms numbered I–IV. Scale bars a, 10 mm; b, c, 1 mm

suckers; modified sucker pedicel pairs fused basally to form lappets; HcLPC 13.0–*14.6*–16.0 (SD 0.8). Each lappet comprised of a dorsal spire-shaped structure with globular tip and a ventral tongue-shaped flap with lobed apex; components joined basally in deep median crease; lappets well defined proximally, less defined and decreasing in size distally.

Tentacle stalks approximately 3–4 × mantle length, slender, oval in cross-section, without suckers. Clubs (Fig. 11d) expanded, tapering to blunt tips; ClLI males 33.3–*41.8*–54.8 ($n=9$, SD 6.1), females 26.9–*37.9*–47.5 (SD 6.5). Clubs with tiny, uniformly sized suckers set in transverse rows of about ten. Largest club sucker diameters similar in both sexes; ClSI males 0.65–*0.75*–0.87 ($n=9$, SD 0.06), females 0.46–*0.66*–0.81 (SD 0.11). Dorsal keel extends slightly beyond sucker-bearing face of club. Tentacular club (Fig. 11e) suckers with symmetrical papillated ring. Internal ring with ~ 15–20 pegs. Four to six intermediate rings with pegs decreasing in size but increasing in number towards external ring. External ring with ~ 70 pegs. Pegs polygonal in shape; surface pitted. Internal surface of rim processes similar in shape to papillate ring pegs.

Gills with 22–24 lamellae per demibranch.

Male reproductive system (Fig. 12a) with testis occupying approximately 50% of posterior mantle cavity. Spermatophore (Fig. 12b, c) cement body bipartite. Cement body posterior part barrel-shaped, with slight median constriction, connecting to sperm reservoir via narrow duct. Cement body anterior part narrower than posterior part, cylindrical, approximately same length as posterior part, connecting to bulbous posterior part via a narrow ridged 'neck'. Ejaculatory apparatus coiled, extending into anterior dilation of spermatophore. Spermatophore length approximately quarter of mantle length on average; SLI 17.9–*23.6*–34.6 (SD 5.1).

Eggs approximately spherical in shape; EgDI 11.5–*14.3*–20.8 ($n=9$, SD 2.8).

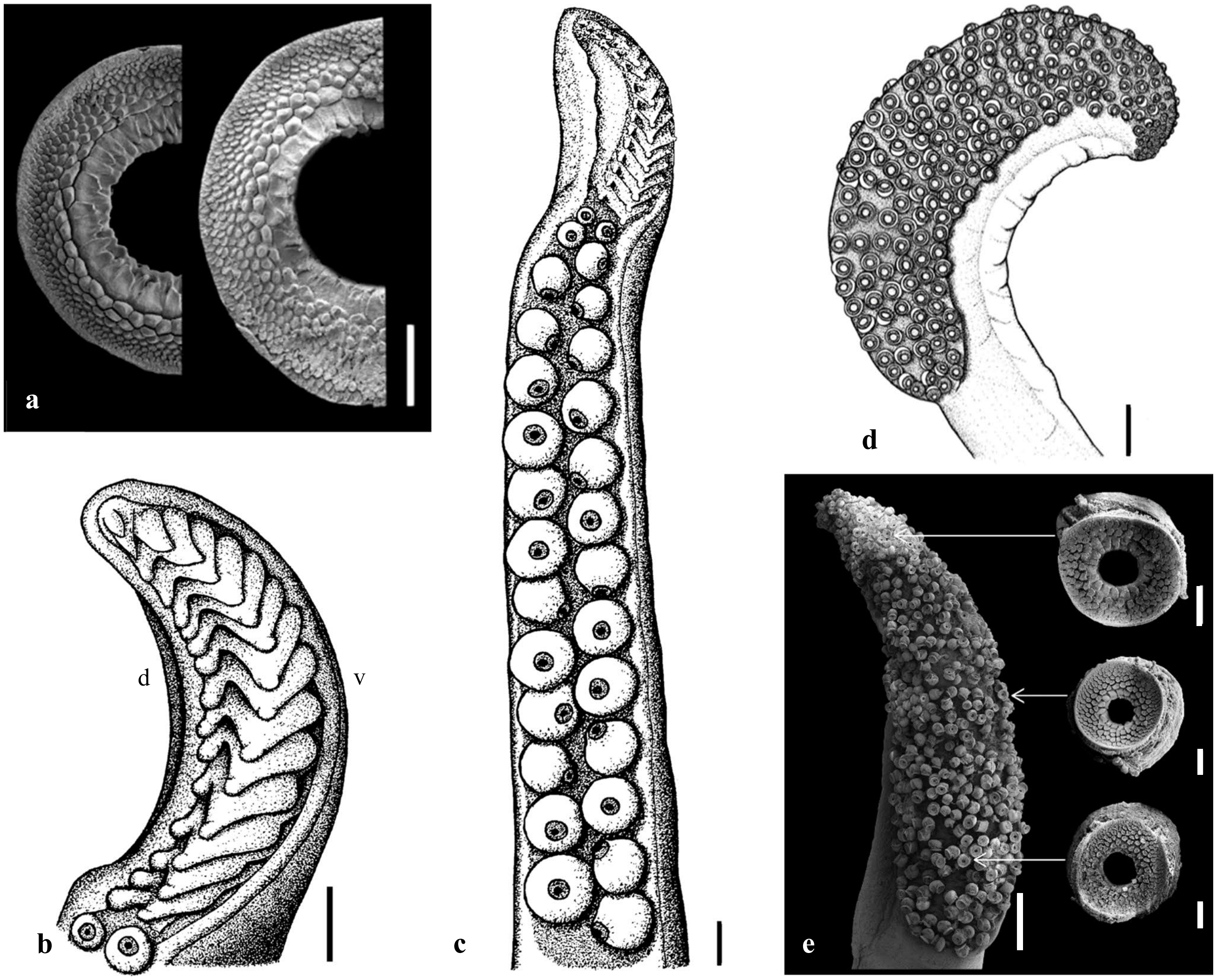

Fig. 11 *Sepioloidea virgilioi* sp. nov.: **a** SEM images: left, portion of Arm III sucker rim, NMNZ M.330520, ♂ paratype, 30 mm ML; right, portion of Arm IV sucker rim, NMNZ M.330522, ♀ paratype, 52 mm ML; **b** hectocotylised left Arm IV distal tip, oral view, NMNZ M.015786, ♂, 29 mm ML; **c** hectocotylised left Arm IV, oral view, NMNZ M.015786, ♂, 29 mm ML; **d** right tentacular club, NMNZ M.84771, ♂, 21 mm ML; **e** SEM images left tentacular club (left image) and club suckers (right images), NMNZ M.330522, ♀ paratype, 52 mm ML. Abbreviations: *d*, dorsal; *v*, ventral. Scale bars a, 100 µm; b–d, 1 mm; e, club 1 mm, suckers 50 µm

Upper and lower beaks (Fig. 13a–c) transparent at posterior margin, darkening to brown then black towards beak tips. Lower beak (Fig. 13a, b) with beak height slightly shorter than half baseline length. Roughly one-third of baseline length extends beyond rostral tip. Hood length half crest length; hood closely adherent to crest. Jaw angle obtuse. Wing length subequal to beak height. Minimum wing width slightly shorter than maximum wing width. Lower rostral length just over a quarter of beak height. Upper beak (Fig. 13c) height roughly half beak length. Hood clear of crest posteriorly, with hood height a quarter of beak height. Upper rostral length over one-third crest length. Rostral tip blunt. Jaw angle almost 90°.

Radula (Fig. 13d) with rows of seven teeth. Rachidian teeth almost twice the length of first lateral teeth, triangular, with base width equal to mesocone height; proximal and lateral margins concave; underside strongly indented medially. First lateral teeth weakly bicuspid; mesocone narrow, shorter than rachidian teeth; outer lateral cusp broad; lateral cusp about a quarter mesocone height. Second lateral teeth unicuspid, similar in height to rachidian teeth; broad basally, directed medially; outer margin nearly straight between base and mesocone tip; inner margin approximately vertical; outer margin approximately 45° from tip to base. Marginal teeth simple, curved proximally, straight distally, longer than rachidian teeth.

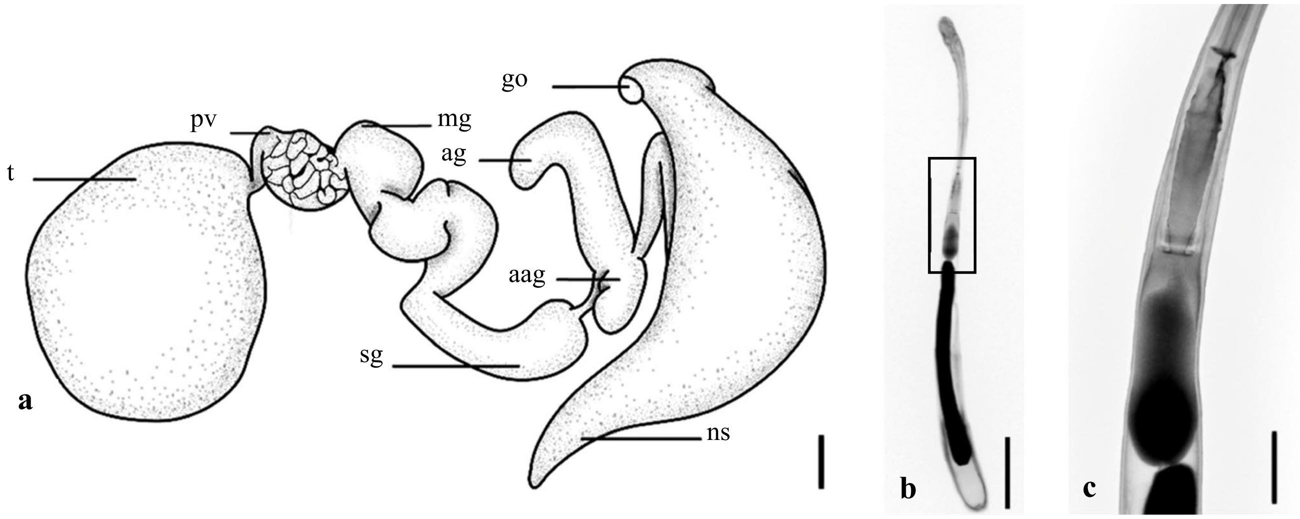

Fig. 12 *Sepioloidea virgilioi* sp. nov. NMNZ M.330520, ♂ paratype, 31 mm ML: **a** male reproductive system; **b** whole spermatophore, cement body outlined; **c** enlargement of cement body. Abbreviations: *aag*, appendix of accessory gland; *ag*, accessory gland; *go*, genital opening; *mg*, mucilaginous gland; *ns*, Needham's sac; *pvd*, posterior vas deferens; *sg*, spermatophoric gland; *t*, testis. Scale bars a, 2 mm; b, 1 mm; c, 500 µm

Preserved specimen colouration varies from pale cream through to dark brown. Chromatophores (Fig. 3c) tiny dots, dark brown/purple, evenly distributed across dorsal surface of mantle, fins, head, and along Arms I, II, and III; fewer on ventral surfaces of the mantle, fins, head, and along Arms IV. Chromatophores present on aboral surface of tentacle club; small and densely set near tip, larger and very sparse proximally, extending along stalk for 150% club length.

Type locality: Auckland Islands, New Zealand, 50° 40′ S, 167° 06′ E, 367–528 m.

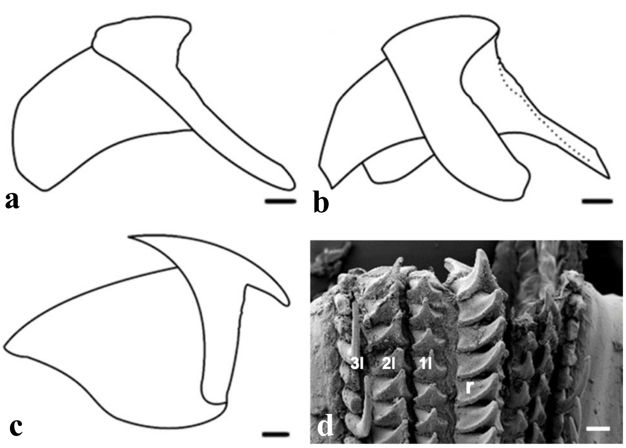

Fig. 13 *Sepioloidea virgilioi* sp. nov.: **a** lower beak, lateral view, NIWA 106067, ♀, 33 mm ML; **b** lower beak, oblique view, specimen as in a; **c** upper beak, lateral view, specimen as in a; **d** SEM image of radula, NMNZ M.330527, ♀, 48 mm ML. Abbreviations: *r*, rachidian tooth; *1 l*, first lateral tooth; *2 l*, second lateral tooth; *3 l*, third lateral (or marginal) tooth. Scale bars a–c, 1 mm; d, 100 µm

Distribution (Fig. 1d): Southwest Pacific, New Zealand, including Auckland Islands and Chatham Rise; 73–911 m.

Remarks: Of the known sepiadariids, *S. virgilioi* sp. nov. is superficially most similar to *S. magna*. Table 6 below compares the quantitative characters between these species. It should be noted that due to material availability at the time of its description, the *S. magna* male data are based on a single specimen (Reid 2009). At maturity, *S. virgilioi* sp. nov. is smaller than the *S. magna* holotype specimen (male *S. virgilioi* sp. nov. ~ 37 mm ML *v. S. magna* ~ 46 mm ML); although females are more similar in size (female *S. virgilioi* sp. nov. ~ 59 mm ML *v. S. magna* ~ 62 mm ML $n = 7$). The chromatophore arrangement is also similar, with both species pale in colour, with tiny, sparsely distributed chromatophores (Fig. 3c). The two species differ, however, in arm and tentacle club morphology, and hectocotylus structure.

All arm suckers in *S. virgilioi* sp. nov. are biserial (Fig. 10d, e), and the club suckers are arranged in ~ 10 per transverse row (Fig. 11d). In *S. magna*, the arm suckers are biserial basally, tetraserial distally, and club suckers are arranged with ~ 40 per transverse row (Reid 2009; supported by examination of AM C.593493). Males of both species exhibit enlarged arm suckers. In *S. virgilioi* sp. nov., the suckers are enlarged midway along all arms (although to a lesser extent on Arms IV), with sucker pairs 5 and 6 often largest (Fig. 10d); in *S. magna*, the suckers are enlarged on Arms II and III (and to a lesser extent on Arms IV), from the basalmost 2 or 3 sucker pairs.

The hectocotylus morphology also differs between the two species. The hectocotylus of *S. virgilioi* sp. nov. is modified only on the distal quarter of the arm (Fig. 11c); its two-structure lappets consist of a spire-like dorsal component

Table 6 Comparison of counts and measurements of *Sepioloidea virgilioi* sp. nov. and *Sepioloidea magna*; numbers in bold indicate distinct differences

Measurement/count	*Sepioloidea virgilioi* sp. nov. males	*Sepioloidea magna* male	*Sepioloidea virgilioi* sp. nov. females	*Sepioloidea magna* females
ML	26.0–30.3–33.0	45.7	36.0–49.2–56.0	39.5–30.3–33.0
MWI	72.7–97.6–121.4	81.0	66.1–89.0–108.3	75.0–87.5–96.7
FWI	13.3–19.8–27.3	15.5	17.3–25.1–34.0	10.5–18.0–25.5
FIIa	20.0–26.4–36.7	20.6	14.5–20.2–30.0	22.5–26.0–29.9
FII	**45.5–52.1–61.3**	**21.9**	46.2–58.4–65.0	-
FuLI	40.0–56.1–65.5	53.6	37.0–51.1–61.1	48.5–61.2–72.7
FFuI	16.1–24.8–33.3	32.8	16.7–22.4–30.0	25.0–28.4–30.7
HLI	66.7–82.3–100.0	70.9	67.9–76.0–81.5	55.4–71.2–89.6
HWI	63.3–87.9–100.0	72.6	58.9–75.4–87.5	56.5–71.0–80.0
EDI	16.7–21.5–26.9	17.7	13.0–16.8–22.5	13.1–15.8–20.2
AL1I	53.3–68.3–82.1	65.6	48.2–63.3–74.5	69.8–75.5–80
AL2I	66.7–79.2–96.6	76.6	51.9–61.4–70.8	67.9–81.7–96.6
AL3I	70.0–84.0–107.1	78.8	57.7–73.5–87.5	76.7–87.1–101.3
AL4I	66.7–89.0–106.9	78.8	62.5–77.0–88.9	71.6–84.6–91.7
ASIn1	5.3–6.5–7.4	4.16	2.0–2.4–3.0	2.3–2.7–3.5
ASIn2	5.7–7.0–8.2	6.35	2.0–2.4–3.1	2.3–2.7–3.5
ASIn3	6.1–6.9–8.1	6.35	2.2–2.6–3.3	2.4–2.9–3.3
ASIn4	4.6–5.9–8.2	3.06	2.0–2.4–3.0	2.2–2.6–3.3
ASC1	**37–45–50**	**76**	**56–62–65**	**100–119–134**
ASC2	**45–48–51**	**80**	**56–64–75**	**114–128–134**
ASC3	**39–50–55**	**100**	**65–70–80**	**130–143–152**
ASC4	**43–54–64**	**104**	**63–70–76**	**122–141–166**
ClLI	33.3–41.8–54.8	54.7	26.9–37.9–47.5	58.2–66.0–75.1
ClRC	6–8–9	-	9–10–11	39–41–42
ClSI	0.7–0.8–0.9	-	0.5–0.7–0.8	0.3–0.4–0.5
EgDI	-	-	11.5–14.3–20.8	15.3–17.3–20.8
HcMLI	20.8–27.4–34.6	~50	-	-

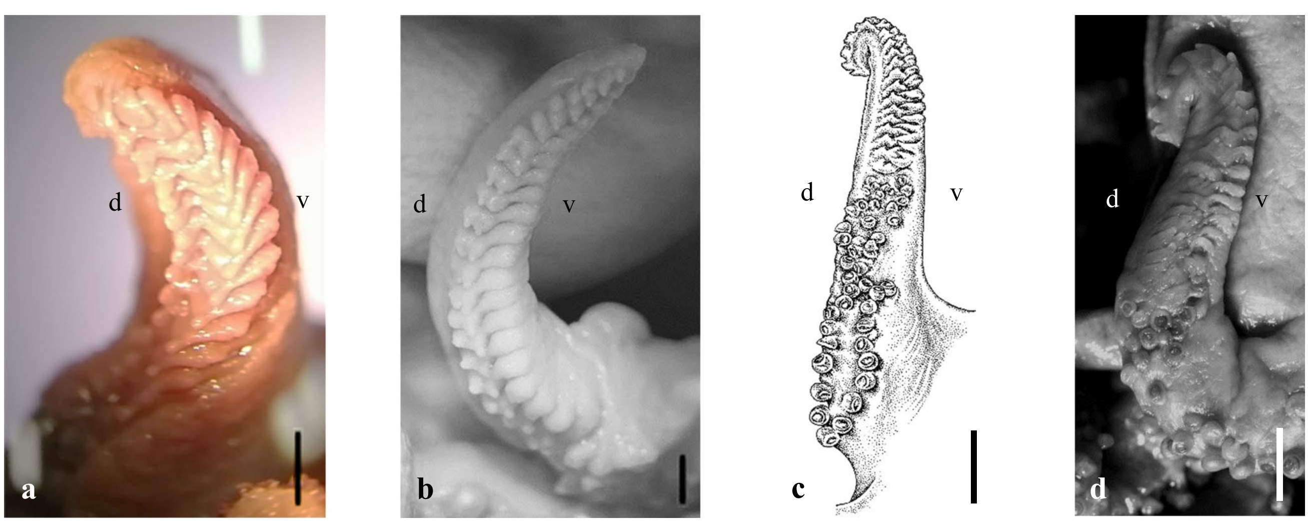

Fig. 14 Comparison of hectocotylus from *Sepioloidea virgilioi* sp. nov. and *Sepioloidea magna*: **a** *S. virgilioi* sp. nov. hectocotylus, NIWA 015786 ♂, 29 mm ML; **b** *S. magna* hectocotylus, AM C.593493, ♂, 62 mm ML; **c** *S. magna* hectocotylus illustration from Reid (2009: Fig. 4A), NTM P.41686, holotype ♂, 45.7 mm ML; **d** *S. magna* hectocotylus photograph M. Sherwood, NTM P.41686, holotype ♂, 45.7 mm ML. Abbreviations: *d*, dorsal; *v*, ventral. Scale bars a, b, 1 mm; c, d, 5 mm

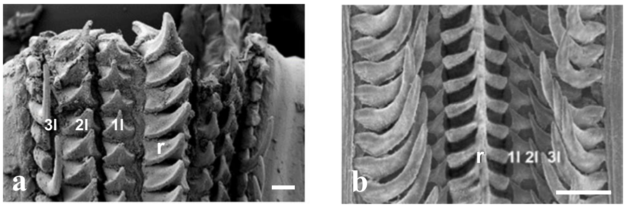

Fig. 15 Comparison of radulae SEM images from *Sepioloidea virgilioi* sp. nov. and *Sepioloidea magna*: **a** *S. virgilioi* sp. nov. radula, NMNZ M.330527, ♀, 48 mm ML; **b** *S. magna* radula from Reid (2009: Fig. 4C), NTM P.1387, paratype ♀, 56 mm ML. Abbreviations: *r*, rachidian tooth; *1 l*, first lateral tooth; *2 l*, second lateral tooth; *3 l*, third lateral (or marginal) tooth. Scale bars a, 100 µm; b, 200 µm

and a tongue-shaped ventral component (Fig. 11b, 14a), each with rounded distal tips. In *S. magna* (Fig. 14b–d), the modified portion of the hectocotylus begins approximately halfway along the arm, and its two-structure lappet consists of a bilobed dorsal component, each lobe with pronounced tip, and a simple, ridge-like ventral component.

This difference is not clearly apparent based on the illustration of the hectocotylus in the original *S. magna* description (Reid, 2009: Fig. 4A) and reproduced here as Fig. 14c. As can be seen from the photograph of the hectocotylus of the submature (45.7 mm ML) holotype specimen (Fig. 14d) (and the only male available at the time the species was described), the hectocotylus is not in good condition, making accurate interpretation difficult. While the hectocotylus image shown in Fig. 14b was taken from a mature specimen collected at some distance south of the *S. magna* type locality (off Broome, Western Australia, 17°17′S, 120°12′E, 304 m *v.* the *S. magna* type locality in the Arafura Sea 9°47′S, 130°26′E, 225 m), AM C.593493 conforms in all respects to *S. magna.* The collection and examination of more mature male *S. magna* specimens from the type locality will be important for determining the reliability of these observations.

From the examination of the single specimens from each of these *Sepioloidea* species, it appears that there are distinct differences in radula rachidian teeth morphology. In *S. virgilioi* sp. nov. (Fig. 15a), the rachidian teeth are more robust and broader basally and are distinctly concave underneath, while in *S. magna* (Fig. 15b), the rachidian teeth have very wide, narrow, rectangular bases. Examination of additional specimens of each species are needed to determine whether these differences are consistent among taxa or simply reflect intraspecific variation.

Further differences between *S. virgilioi* sp. nov. and the other recognised *Sepioloidea* are provided in Remarks for *S. jaelae* sp. nov. and are summarised in Table 7 to facilitate identification.

It is possible that many early records of 'deep-water' *S. pacifica* may refer to *S. virgilioi* sp. nov. (Dell 1959: 2) reported finding these 'larger' specimens (up to 40 mm ML compared to the 'typical' 20 mm ML) from depths greater than 75 fathoms (137 m). He hypothesised that this may be an indicator of size classes, with older individuals living in deeper water. In the only *S. pacifica*-focused research to date, Hurst (1969: 8–10, Fig. 3) described a clear separation in size class between smaller shallow-water specimens (< 140 m) and larger deep-water specimens (collected at 140 m and 210 m), which were approximately double the mantle width and length of the shallow-water group. Hurst was able to photograph one of these deep-water specimens in the short time it was kept in aquaria after live capture; this is most likely a live *S. virgilioi* sp. nov. specimen (Fig. 9a). Powell (1979: 440) may not have been aware of any differences according to depth when he listed the *S. pacifica* depth range as 75–300 fathoms. Unfortunately, none of these larger, deep-water specimens were lodged in museum collections for further

Table 7 Summary of *Sepioloidea* diagnostic characters. *Sepioloidea lineolata* (Quoy & Gaimard, 1832) has been excluded because the details for this species are unknown. It requires full redescription; however, it is the only species in the genus to have longitudinal lines along mantle and head, and fringed anterior dorsal mantle margin

Species	Diagnostic structure		
	Hectocotylus	Tentacle club suckers	Arm suckers
Sepioloidea jaelae sp. nov	Modified for ~ 50% of arm length Lappets (~ 16) symmetrical; each with paired globular tips	~ 6 suckers per transverse row No sucker enlargement	Biserial
S. magna Reid, 2009	Modified for ~ 50% of arm length Lappets (~ 22) asymmetrical; bilobed ventrally, lobe tips pronounced, ridge-shaped dorsally	~ 40 suckers per transverse row No sucker enlargement	Biserial proximally; tetraserial distally
Sepioloidea pacifica (Kirk, 1882)	Modified for ~ 50% of arm length Lappets (~ 20) asymmetrical Lappets bilobed ventrally, wedge-shaped dorsally	~ 5 suckers per transverse row Suckers largest midway along dorsal club margin	Biserial
Sepioloidea virgilioi sp. nov	Modified for ~ 25% of arm length Lappets (~ 15) asymmetrical; spire-shaped ventrally, tongue-shaped dorsally	~ 10 suckers per transverse row No sucker enlargement	Biserial

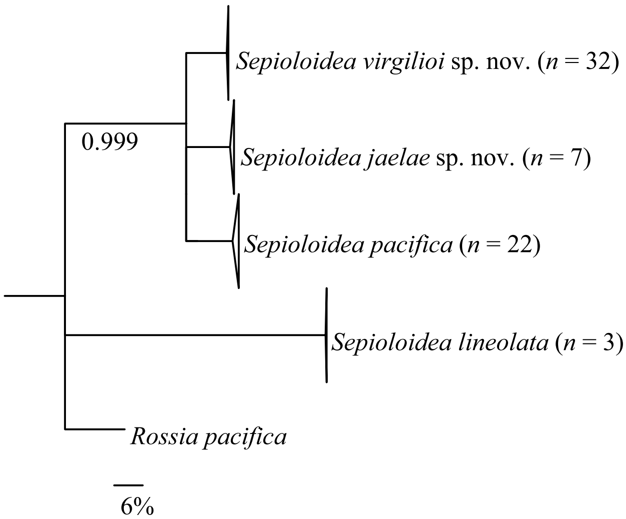

Fig. 16 Maximum-likelihood phylogeny based on cytochrome *c* oxidase subunit I (COI) for specimens of *Sepioloidea*, morphologically identified as *S. jaelae* sp. nov., *S. pacifica*, and *S. virgilioi* sp. nov., with *Rossia pacifica* used as an outgroup, with 1000 bootstrap replicates

examination. The depths at which confirmed *S. pacifica* specimens have been captured are all shallower than those of *S. virgilioi* sp. nov. (all collected between 73 and 911 m). For example, the type locality of Kirk's holotype (and subsequently, Dell's neotype) is Wellington Harbour, New Zealand, which has a maximum depth of 21 m. Dell's voucher specimens from 1952 were from Lyttelton Harbour with a maximum depth of 12 m. All 30 + confirmed *S. pacifica* lots loaned for this study were collected at < 55 m depth. Reid (2009: 108) quoted a 15–550 m depth range for *S. pacifica* based on the data cited by Powell (1979: 440). It is possible that the deeper end of this depth range may correspond to collection records for *S. virgilioi* sp. nov. and/or *S. jaelae* sp. nov. rather than *S. pacifica.* The present results suggest that *S. pacifica* is a smaller-bodied, shallow-dwelling species and *S. virgilioi* sp. nov. is a larger-bodied, deep-dwelling species.

Molecular results

The aligned 658 bp sequences showed no insertions, deletions, or stop codons. Five separate clades were identified in the phylogeny, representing five sepioloids: *S. pacifica*, *S. lineolata*, *S. virgilioi* sp. nov., *S. jaelae* sp. nov., and the outgroup species, *Rossia pacifica* (Fig. 16).

Sepioloidea virgilioi sp. nov. was represented by the most numerous ($n = 32$) and most geographically widespread samples. Even with such wide coverage, *S. virgilioi* sp. nov. showed the lowest intraspecific distances (Table 8). The fewest specimens from New Zealand waters were available for *S. jaelae* sp. nov. ($n = 7$). Both *S. jaelae* sp. nov. and *S. pacifica* had relatively high maximum intraspecific distances (*S. jaelae* sp. nov.: 1.42%; *S. pacifica*: 1.57%) compared with *S. virgilioi* sp. nov. and *S. lineolata* (*S. virgilioi* sp. nov.: 0.18%; *S. lineolata*: 0.31%). High interspecific distances were found within the New Zealand *Sepioloidea*, with a minimum of 11.09% between *S. pacifica* and *S. jaelae* sp. nov. and a maximum of 14.29% between *S. pacifica* and *S. virgilioi* sp. nov.. The Australian *Sepioloidea* species *S. lineolata* had relatively higher interspecific distances with each of the New Zealand *Sepioloidea* species (mean ~ 25%).

The maximum-likelihood phylogeny (Fig. 16) shows high support for the distinction among all New Zealand *Sepioloidea* species and the Australian *S. lineolata* (bootstrap value of 0.999).

The maximum-likelihood bPTP analysis supported the morphological determination of the two new species in this study (*S. virgilioi* sp. nov. and *S. jaelae* sp. nov.; Fig. 17).

Discussion

To date, all *Sepioloidea* specimens collected in New Zealand waters and identified to species have been attributed to a single nominal species, *S. pacifica* (Spencer et al. 2016). Through the examination of over 600 specimens, plus the sequencing of an additional 61 specimens, this study confirms the presence of two novel species in addition to *S. pacifica* in New Zealand waters. Morphological examination of all *Sepioloidea* species (except *S. lineolata*) provided the basis for a summary of reliable diagnostic characters (Table 7). In addition, this study includes molecular sequences of *S. pacifica* and both novel species, which support the morphological findings (Fig. 16). By taking this integrative taxonomic approach, the recognition of two new species, *S. virgilioi* sp. nov. and *S. jaelae* sp. nov., is robustly supported by multiple lines of evidence. Additionally, this study reports on some additional morphological details for a new, fully mature male *S. magna* specimen (AM C.593493) that has become available since the species' description in 2009. Morphological information and images obtained from this specimen provided more detail upon which to build diagnostic species descriptions.

As a result of this work, *Sepioloidea* is now known to contain five nominal species, with representatives in New Zealand and Australian waters, as well as a taxon identified as *Sepioloidea* cf. *pacifica* from the Sala y Gómez Submarine Ridge. These comprise both small-bodied taxa (*S. jaelae* sp. nov., *S. lineolata*, and *S. pacifica*) and relatively large-bodied taxa (*S. magna* and *S. virgilioi* sp. nov.). While many morphological features unite these species (e.g., narrow fins, hectocotylised left Arms IV, biserial arm suckers,

Table 8 Percent intraspecific (in bold) and interspecific distances for cytochrome *c* oxidase subunit I (COI) for four species of *Sepioloidea*

	S. jaelae sp. nov.			*S. pacifica*			*S. virgilioi* sp. nov.			*S. lineolata*		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
S. jaelae sp. nov	**0.00**	**0.50**	**1.42**	–	–	–	–	–	–	–	–	–
S. pacifica	11.09	12.37	13.12	**0.00**	**0.34**	**1.57**	–	–	–	–	–	–
S. virgilioi sp. nov	11.55	12.21	13.82	12.20	13.12	14.29	**0.00**	**0.02**	**0.18**	–	–	–
S. lineolata	23.56	25.18	26.45	24.60	26.83	27.94	24.05	25.54	26.63	**0.00**	**0.10**	**0.31**

locking cartilage structure, and mantle and head fusion) and support their grouping within *Sepioloidea*, it would be useful to undertake a thorough examination of Australian Sepiadariidae. In particular, *S. lineolata* requires redescription because some morphological details of this species are not yet well reported, and some of its known characters differ from those of all other *Sepioloidea* species (such as the fringed anterior mantle margin and the chromatophore pattern of longitudinal lines). Based on COI sequence data, the three species from New Zealand waters appear closely related, but their relationship to *S. lineolata* was not resolved (Fig. 16). Since this analysis was limited to a single mitochondrial gene, the inclusion of additional genes (including nuclear genes) may be required to fully understand the relationships among species in this family. In addition, now that more fully mature *S. magna* specimens are available in museum collections (in particular, the Melbourne Museum, Australia, Reid pers. comm.), more comparative material, particularly of males, can be examined to look for additional morphological differences.

Distribution: Despite the potential for bias due to sampling and collection effort, the records of the New Zealand *Sepioloidea* species appear to reflect three different maximum depths. Like *S. magna*, both *S. virgilioi* sp. nov. and *S. jaelae* sp. nov. have been collected from deeper waters (73–911 m and 0–440 m, respectively) than the inshore species *S. pacifica* (< 55 m) and *S. lineolata* (< 100 m). Unfortunately, because it is unclear from collection data whether those specimens purportedly collected within a range including 0 m occurred intertidally or were collected at the surface (possibly at night), the suspected depth differences among the three species may actually be more discrete than is apparent from the data. The apparent maximum depth distribution of the three New Zealand species align with different habitats: *S. pacifica* is only reported from inshore waters (Fig. 1b); *S. jaelae* sp. nov. has mainly been collected offshore in deeper waters, particularly within in the Southern Taranaki Basin (Fig. 1c); and *S. virgilioi* sp. nov. presently appears to have the widest distribution offshore, having been collected from deep waters (to 911 m) near the Auckland Islands and along the Chatham Rise (Fig. 1d). Occasionally, more than one *Sepioloidea* species has been collected in a single trawl. This, along with the overlaps in collection depths between species, indicates sympatry. For example, barcoded *S. pacifica* (NIWA 142705) and barcoded *S. jaelae* sp. nov. (NIWA 157615) were originally in the same specimen lot and were collected at the same time and location at 45–48 m depth; barcoded *S. jaelae* sp. nov. (NIWA 157614) and barcoded *S. virgilioi* sp. nov. (NIWA 106088) were originally in the same specimen lot and were collected at the same time and location at 357–367 m. Interestingly, one female specimen identified as *S. pacifica* has also been collected from Waitangi Wharf in the Chatham Islands. It is possible that this specimen represents a once-connected, but now isolated population of *S. pacifica*, but the collection of additional material is needed to determine whether this is, indeed, the case. Based on a single record only, little inference should be drawn but is worthy of mention. In terms of geographical distribution, both *S. virgilioi* sp. nov. and *S. jaelae* sp. nov. have only been recorded New Zealand waters to date, and do not overlap with either *S. lineolata* or *S. magna* from Australia.

The Chatham Islands are presently connected to the New Zealand mainland by the Chatham Rise, which is relatively shallow compared with the surrounding seafloor (~ 1000 m depth compared to the ~ 3000 m trenches along the north and south margins) but still far below the known depth range for *S. pacifica* at any life stage. As the Chatham Rise began submerging along with the Zealandia continent relatively recently at the end of the Cretaceous period (Stilwell and Consoli 2012), the rise could have provided a habitat for ancient *S. pacifica*, thus resulting in the formation of this isolated population when the water depth increased. Another explanation may be that a natural gene flow continues to exist between the two populations, but that seems highly unlikely due to the apparent depth limits of *S. pacifica* and current depth of the Chatham Rise. These limits are suggested by the very little overlap of *S. pacifica* into the offshore habitat of *S. jaelae* sp. nov. and the absence of *S. pacifica* from deep water records (i.e., the depth range of *S. pacifica* is unlikely to be a simple artefact of collection effort). In future, molecular data could be compared from the mainland and Chatham Islands populations to provide insight into whether/when these populations may have diverged. The absence of deep-water *S. pacifica* specimens from collections to date—and by extension, the partial stratification of these three species

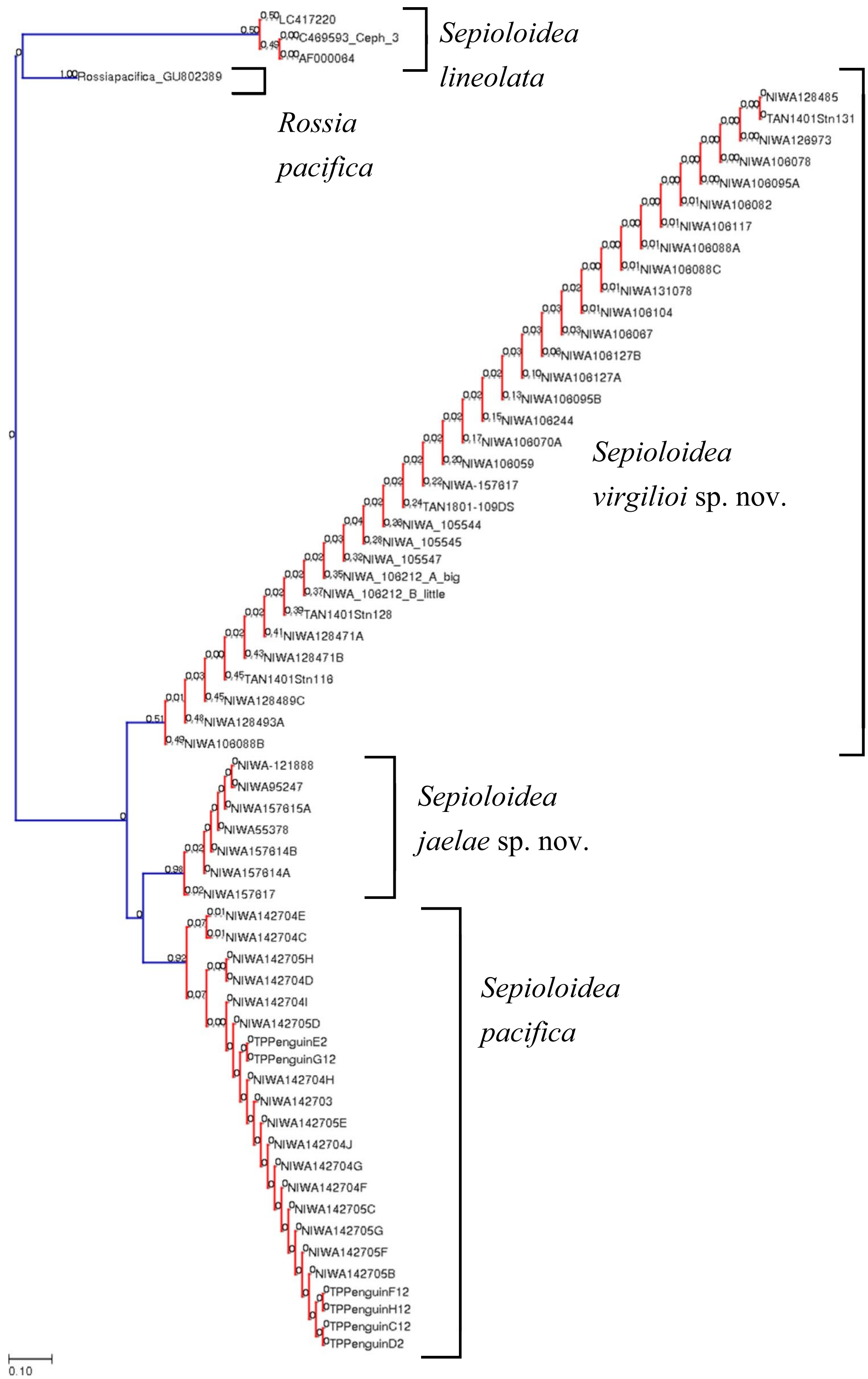

Fig. 17 Maximum-likelihood solution from the Bayesian Poisson tree processes (bPTP) analysis of cytochrome *c* oxidase subunit I (COI) sequences for *Sepioloidea*. Outgroup *Rossia pacifica* also shown. Blue bars indicate sequences that delineate the species boundaries recognised here, red lines indicate sequences that represent the same species. This analysis supports the recognition of four distinct species in *Sepioloidea*: *S. pacifica*, *S. virgilioi* sp. nov., *S. jaelae* sp. nov., and *S. lineolata* (*S. magna* sequences are not available)

by depth—could be due to a number of specific adaptations (Summers 1983) or biogeographic history.

Ecology and biology: Very little is known about the biology and ecology of New Zealand *Sepioloidea* and this would be a worthy subject of future research. Dell (1959) stated that it is 'fairly certain' that *S. pacifica* shelters in mud or debris diurnally and is active nocturnally. This is supported by benthic sampling efforts around New Zealand, which showed *S. pacifica*'s presence throughout the continuum of sandy to muddy habitats (Knight 1974). Sampling of different bathymetric habitats (i.e., from inshore to deep canyons) off the Otago peninsula found that *S. pacifica* only occurred in inshore sandy and inshore muddy sand habitats (Probert et al. 1979). This was supported in later research that showed all taxa within the family Sepiadariidae (*Sepioloidea* and its sister taxon *Sepiadarium*) are known to bury in sand during the day and emerge at night (Reid and Jereb 2005; Reid 2016). There is little evidence to cast doubt on the assumption that *S. pacifica* and the two novel species described in this study are also benthic animals. Whether juvenile *Sepioloidea* species have a planktonic stage is a separate matter that is not yet known.

Sepiolids are frequently reported in the diets of predators. An example of this link is the group of *S. pacifica* genetic sequences labelled 'penguin' (Fig. 17). The Fiordland penguins (*Eudyptes pachyrhynchus* Gray, 1845) from which gut sample specimens were obtained were studied by Poupart et al. (2019) and were found to forage from early morning to afternoon at an average depth of 22 m. This infers that these penguins are able to locate and feed on the shallow-dwelling *S. pacifica* despite their strategy of hiding beneath sand during the day.

The only research known to date that involved the rearing of live New Zealand *Sepioloidea* was a dissertation on the biology of *S. pacifica* (Hurst 1969). Hurst (1969: 55) described the hatchlings of *S. pacifica* as 'similar to the adult' and that they were capable of active swimming but tended to settle on the aquarium substrate. The distributions of *Sepioloidea* species may be limited by a strong association to the benthos from early life, as has been discussed by Bello (2017) regarding the endemism of large-egged *Sepiola* species in the Atlantic Ocean and Mediterranean Sea. Furthermore, this could possibly be limited further by substrate preferences, such as that of *S. pacifica* and its association with sandy substrates (Knight 1974; Probert et al. 1979). The large eggs seen in the oviducts of preserved *S. jaelae* sp. nov. (average EgDI 13.1) and *S. virgilioi* sp. nov. (average EgDI 14.3) suggest that the hatchlings are also relatively large and well-developed. This is a common reproductive strategy in sepiolids (Mangold 1987).

DNA barcoding: Specimens were available from all three species of *Sepioloidea* found in New Zealand waters for genetic analysis, which allowed for the direct comparison of both morphological characters and the DNA barcode region. The barcoding results support the separation of all three *Sepioloidea* from New Zealand (bootstrap support 0.999), which are also distinct from the only sequenced species from this genus found in Australian waters (Fig. 16). This is the first study to provide sequence data for the nominal New Zealand taxa in this genus. However, the relationships between the New Zealand *Sepioloidea*, and between these species and the Australian *Sepioloidea*, remain unresolved. In order to clarify these relationships, sequence data from *S. magna* may prove valuable, and perhaps sequencing additional mitochondrial and nuclear genes could provide deeper phylogenetic resolution.

The smallest maximum intraspecific distance was identified in *S. virgilioi* sp. nov. (0.18%) despite being represented by the most numerous and geographically widespread samples ($n=32$) (Fig. 16). The *S. pacifica* and *S. jaelae* sp. nov. specimens both represented smaller geographic ranges but showed larger intraspecific distances (*S. pacifica* with 1.57% maximum intraspecific difference, and *S. jaelae* sp. nov. with 1.42%). These differences could suggest greater mixing of the entire population of *S. virgilioi* sp. nov. within the New Zealand region, or alternatively could indicate a recent bottleneck and/or population expansion outward from a more restricted location.

A DNA barcode gap (as discussed by Meier et al. 2008) was observed within the *Sepioloidea* sequenced in this study (Table 8). The maximum intraspecific difference observed within any single New Zealand species was 1.57% (*S. pacifica*), while the minimum interspecific difference observed was 11.09% (also *S. pacifica*), with the mean pairwise distance between any two New Zealand *Sepioloidea* species falling in the range of 12–14%. Interestingly, the minimum interspecific distances between any New Zealand *Sepioloidea* species and the Australian *S. lineolata* were nearly double, at a minimum of 23.56% (mean 25–27%). Although no conclusions about the higher taxonomy in this family can be made from a single mitochondrial gene, this discrepancy indicates that an integrative taxonomic investigation into the higher classification of these species is warranted. In particular, the Australian *Sepioloidea* require better representation in phylogenetic analyses; despite being recorded from nearly the entire coastline of Australian (Atlas of Living Australia 2020), only three sequences are currently available for *S. lineolata*. Additionally, future studies should include *S. magna* if fresh specimens become available.

Conclusion

Until now, almost all *Sepioloidea* specimens from New Zealand (apart from those few labelled conservatively in collections facilities) were thought to comprise a single species: *S. pacifica*. We now know that at least three species in this genus are present in New Zealand waters. While Reid (2009), among many others, has already called for a comprehensive revision of the phylogeny of Sepioidea, a very worthwhile project of smaller scope within this broader study would be a re-investigation into the systematics of the family Sepiadariidae, its two member genera *Sepioloidea* and *Sepiadarium*, and their relationships. Additionally, the procurement of molecular data from all Sepiadariidae species would be a great help in untangling aspects of Sepiolida phylogenetcs as well as their position within the Order Cephalopoda as a whole—projects that are growing in reliance on DNA yet severely lacking in Sepiadariidae representation.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval No animal testing was performed in this study. All specimens studied were preserved and borrowed from institutions. No animals killed for the purpose of this study.

Sampling and field studies All necessary permits for sampling were obtained by the specimen lending institutions as mentioned in the 'Acknowledgements'. The study is compliant with Convention on Biological Diversity (CBD) and Nagoya protocols.

Data availability The datasets generated during the current study are available from the corresponding author on reasonable request. Genetic sequences are available on the Barcode of Life Data System (BOLD) and GenBank. Zoobank references and museum registration numbers are all provided.

Author contribution All authors contributed to the study conception and design. Material preparation, data collection, and analyses were performed by JS. HB conducted the molecular analyses. The manuscript was written by JS and edited and revised by JS, KB, and HB.

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