Ecology and ontogeny of the cranchiid squid *Teuthowenia pellucida* in New Zealand waters

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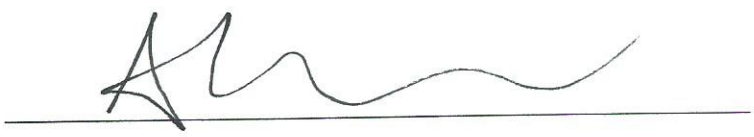
Attestation of Authorship

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.



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Abstract

Teuthowenia pellucida, a species of glass squid, is a cosmopolitan southern sub-tropical species, and is abundantly represented in local New Zealand collections. However, due to the depth at which adult specimens live, little is known about its systematics, biology or trophic importance. Morphological similarities between this and other cranchiid genera at early ontogenetic phases make accurate identification of small specimens difficult. Herein, the morphological changes characterising six pre-adult developmental stages (termed A–F) are reported in detail, as well as adult morphology; new information is provided on fecundity. The retinal structure of *Teuthowenia*'s proportionally large eyes is examined, including photoreceptor length and ommin movement, at various life phases. Finally, a meta-analysis of global predators examines the role of *Teuthowenia* in both photic and aphotic marine ecosystems. These findings comprise a small contribution toward the knowledge of this little-known genus within the Cranchiidae.

Introduction

Around 375 squid species are believed to inhabit the world's oceans (Tree of Life, 2006), from about 80 genera (Young & Vecchione, 2004; Vecchione & Young, 2008). Of these, many spend some or most of their lives in the mesopelagic and bathypelagic environment, commonly known as the deep sea. This environment is commonly defined as the waters below the photic zone (commencing at 200–300 meters' depth depending on geographic location and water clarity). The deep sea is a largely unexplored expanse, and many of its inhabitants have been poorly described or are unknown to science. In order to understand the systematics and biology of these species, it is important to understand their environment.

The deep sea was long considered a barren expanse of ocean with little life; however, after technological advances in the 1950's scientists began to realise that the deep sea was far more diverse than originally thought. Sanders (1968) suggested that species richness increased with depth up to about 2000 meters. Since then, several hypotheses have been suggested to further explain deep-sea richness (Gray, 2001); however, no single explanation is currently accepted. Sanders (1968) described the deep sea as being "biologically accommodated", meaning that diversity was directly related to species competitiveness, rather than physical environmental factors; however, further research showed that the environment has physical variability and species in the deep sea live in a habitat with changing temperature, increased pressure, areas of oxygen depletion, hydrostatic regimes (Levin et al., 2001) and diminished light availability below the photic zone. These environmental factors affect predator–prey interactions, interspecies communication, and mating practices. Species that live in this environment display physical and behavioural modifications that allow them to interact with each other.

Many species that live below the photic zone use bioluminescence (light emitted from the tissue of the organism by chemical or symbiotic means), to communicate, create camouflage, and deter predators. In order to receive and interpret bioluminescent signals, some animals that live in this environment have evolved large eyes, which are sensitive to low levels of light (Land, 1981). Deep-sea cephalopods in particular often possess large, well-developed eyes; the eyes of the squids *Mesonychoteuthis hamiltoni* and *Architeuthis dux* are the largest in the animal kingdom (Nilsson, Warrant, Johnsen, Hanlon & Shashar, 2012). These structures can effectively detect bioluminescent patterns created by the movement of large predators, such as sperm whales, at great distances. Smaller species of deep-sea squid also have relatively large eyes that detect minimal amounts of light and help to maintain effective counter-shading to evade predators (Young & Roper, 1977; Young, Roper & Walters, 1979; Voss, 1985). This method of crypsis uses bioluminescence on the ventral portion of the body to match down-welling light from above. Several families of octopods and squid (including the Cranchiidae) also have largely transparent tissues, which further improve crypsis.

Cranchiids are commonly known as 'glass' squid, a name arising from the transparent appearance that members of the family exhibit for a large majority of their life, and some through adulthood (Voss, 1980; Piatkowski & Hagen, 1994). Despite cranchiid abundance, little work has been done on either the systematics or ecology of the genera in this family (Voss, 1980; Arkhipkin, 1996). Adult cranchiids range in size from 100 mm mantle length (ML) (*Helicocranchia*) to over 2 meters ML (*Mesonychoteuthis*) (Young & Mangold, 2008), and representative species are found in all oceans. Several members of the family possess extremely large eyes, both absolute (*e.g*., *Mesonychoteuthis*) and relative (*e.g*. *Teuthowenia*), and species from all genera possess photophores (Herring, Dilly, & Cope, 2002). Although many squid

migrate vertically to greater depths during the day (Murata & Nakamura, 1998; Rosa & Seibel, 2010), cranchiids (which may also display diel migration behaviours) undergo ontogenetic descent, with larval animals living in the epipelagic zone, and later descending to deeper waters (Voss, 1980).

This migration behaviour has been documented in the local cranchiid species *Teuthowenia pellucida* (Voss, 1985), which is found in southern sub-tropical deep sea environments circumglobally. The other two *Teuthowenia* species, *T. maculata* and *T. megalops*, are found in the central and north Atlantic. The original aim of this study was to investigate the possibility of multiple *Teuthowenia* species in New Zealand waters; however, upon confirming *T. pellucida* as the only resident species, additional aspects of its biology were investigated. Below, *T. pellucida* is described throughout its development, the retinal structure of the eye throughout maturation is examined to investigate whether it exhibits particular modifications for deep-sea life, and the genus' global role in the diets of predators is analysed.

Literature Review

The systematic history of *Teuthowenia pellucida* (and most of the other cranchiids) has been convoluted, made more complex by several instances of larval stages being erroneously described as new species. The genus *Teuthowenia* was originally described by Prosch (1847), as '*Owenia',* a subgenus of *Cranchia*. Chun (1910) officially changed the genus name to *Teuthowenia*, which included the original species *T. megalops* and the newly described *T. 'antarctica'* (= *Galiteuthis glacialis).*

Teuthowenia pellucida was first described by Chun (1910) from a specimen caught in the South Atlantic, which he named *Desmoteuthis pellucida*. The animal had a ML of 77 mm, oval-shaped eyes on stalks, and a gelatinous, transparent mantle (Chun, 1910). '*Desmoteuthis'* (later split into *Teuthowenia* and *Taonius*) was believed to differ from other cranchiid genera, such as *Taonius* and *Helicocranchia*, due to differences in fin shape. In 1912, Berry suggested that several species (from across several genera, including *Taonius*, *Leachia* and *Desmoteuthis*) all closely resembled existing members of the genus *Megalocranchia* and were therefore re-classified into that genus (Berry, 1912). In 1916, Berry then described a new species found off the Kermadec Islands, which he called '*Megalocranchia' pardus* (= *Liguriella pardus*). At this time, Berry also suggested that *Desmoteuthis* and *Taonius* were synonymous and that *Taonius* was the appropriate classification, but that one species ('*D. ternera'* Verrill, 1881 [= *Teuthowenia megalops*]) be removed from this genus and be placed in the newly formed genus '*Verrilliteuthis'* Berry, 1916 (= *Teuthowenia*). In 1959, Dell described a new species, *Megalocranchia richardsoni*, which differed from *M. pardus* due to significantly larger eyes; stating that, despite a significant difference in size, the two were different species rather than the smaller *M. pardus* being a juvenile phase.

During a research trawl in South African waters, Robson (1924) discovered a cranchiid squid that was described as having the body shape, arms and suckers similar to *Megalocranchia* or '*Desmoteuthis'*; however, several key differences, most notably a lack of fins, prevented Robson from attributing the specimen to either of those genera. Instead, the animal was placed in a new genus, '*Anomalocranchia'*, and named '*A. impennis'* (= *Teuthowenia pellucida*). This genus was later synonymised with *Sandalops* Chun (Nesis, 1974), and still later found to be a junior synonym of *Teuthowenia* (Voss, 1980). In 1966, Clarke reclassified many of the known cranchiids into the genus *Taonius*, including '*Desmoteuthis' pellucida* Chun, 1910, and *Megalocranchia richardsoni* Dell, 1959. However, Clarke did state that *T. pellucida* could actually be *Taonius megalops* (= *Teuthowenia megalops*) (which had become the designated classification for twelve nominal 'species' of cranchiid squid), due to their very similar appearance.

Voss (1967) discussed the confusion forming amongst the classification of the genera *Megalocranchia*, *Desmoteuthis*, and *Teuthowenia*, stating that species were being created on the basis of missing features that could simply be a developmental difference between larval and adult forms. He concluded that although the species *M. megalops 'australis'* (= *T. pellucida*), a new South African species described herein, exhibited consistently different characteristics from known members of all three genera, it should be designated as *Megalocranchia*, as that was the genus it most closely resembled. This species was later deemed to be the sub-species of '*Verrilliteuthis' megalops* by Nesis (1974) who, in an attempt to simplify the systematic entanglements of the genera *Tanoius*, *Desmoteuthis*, and *Megalocranchia*, combined members of each into '*Verrilliteuthis'* and his new genus '*Vossoteuthis*' (now *Liguriella* and *Teuthowenia*). '*Verrilliteuthis'* contained '*V'. megalops 'australis'* and '*V'. richardsoni* from the waters of the

southern hemisphere and '*V'. megalops megalops*, from the north Atlantic. '*Vossoteuthis'* contained the species *pellucida* and *pardus*, although Nesis admitted that no specimens of the species '*Vossoteuthis pardus'* (previously *M. pardus*), were examined during the reclassification.

'Verrilliteuthis' richardsoni and '*V'. megalops australis* were later both reclassified as *Teuthowenia megalops 'impennis'* (= *Teuthowenia pellucida*) by Imber (1978), who felt that '*Anomalocranchia impennis'* had been originally misplaced into a new genus due to contraction of the mantle. Imber also reinstated the genus '*Fusocranchia'* Joubin (now *Liocranchia* and *Teuthowenia*) for one species that resembled *T. megalops 'impennis'* in shape, but with minor morphological differences. This species was named '*F'. pellucida* and supposedly replaced all species within the genus '*Vossoteuthis'*. Voss (1980) compared this specimen to the type specimen of '*Fusocranchia'* and concluded that there were morphological differences. '*Fusocranchia' pellucida* was therefore deemed a member of *Teuthowenia* along with '*Vossoteuthis pardus'* (Voss, 1980).

In 1980, N. Voss revised all genera in the family Cranchiidae, narrowing the number down to thirteen genera, divided into two sub-families. The genera '*Owenia'*, '*Verrilliteuthis'*, and '*Anomalocranchia'* were all considered junior synonyms of *Teuthowenia*. Voss concluded that this genus contained the three geographically separated species still accepted today, (*T. pellucida*, *T. megalops*, and *T. maculata*). Voss (1985) went on to describe the morphology of these three species in great detail.

Materials and Methods

Specimens were examined from the National Institute of Weather and Atmospheric Research, Ltd (NIWA) and the National Museum of New Zealand Te Papa Tongarewa (NMNZ) in Wellington, New Zealand (Appendix 1). All specimens were fixed in ~4% formalin and stored in 70–80% ethanol. Examinations and illustrations were made using a dissecting microscope with camera lucida. Morphological measures and counts were taken as per Roper and Voss (1983). Tentacle club suckers were imaged using scanning electron microscopy (SEM), after being critical-point dried and sputter-coated in gold–palladium.

Larval and juvenile developmental stages were identified based on morphological differences (outlined in Table 1.1), with divisions made when several physical features changed markedly, or developed where absent in the previous stage (*e.g.*, tubercles first appearing in stage C). Using these criteria, six stages were identified prior to the adult phase. Although chromatophore patterns have been found to have systematic use in young squids (Young & Harman, 1987), the condition of the material examined herein varied considerably, preventing identification of consistent patterns. Chromatophore size and density have been noted where possible.

The fecundity of females was determined by removing the entire ovary of a mature female, separating the eggs from the supportive fibres, and weighing the egg mass; subsets were then counted and weighed in several trials, and the mean of all calculations used to extrapolate the total number of eggs present.

Beaks were removed from preserved specimens, and soft tissues removed. Illustrations were made using a camera lucida attachment and Leica WILD M3B microscope. Beak description terminology follows Clarke (1986).

Tissue Preparation:

Whole eyes were removed from seven preserved specimens of *Teuthowenia pellucida,* which had been fixed in 5% buffered formalin and stored in 70–80% ethanol until processed. Prior to cryosectioning, the eyes were washed several times in Phosphate Buffer Saline (PBS) solution and left for 24 hours, before being stored in a 30% sucrose dissolved in PBS overnight. All eyes were hemisected along the ventro-dorsal midline, sectioning the lens in two; one half of the eye was then frozen in TissueTek cryo-OCT compound. Cross-sections of the eye were taken perpendicular to the equator to obtain antero-posterior retinal samples. A LEICA cryostat machine was employed and set at a thickness of 16–20 µm. Eye sections were transferred to glycerine-coated slides and were stored at -20˚C until stained.

Staining:

Slides were stained using a standard haematoxylin and eosin (HE) staining procedure for contrast of nuclei and cytoplasm. The slides were washed in PBS, hydrated and placed into absolute ethanol for five minutes. The slides were then placed in a solution containing glacial acetic acid, aluminium sulphate, sodium iodate, ethylene glycol and haematoxylin for five minutes. The slides were then washed under running distilled water and stain differentiated in 1% acid alcohol. After rinsing, the slides were dipped in 1% lithium carbonate and then washed in distilled water for five minutes. 1% eosin stain was used for contrast. Following staining, the

slides were rinsed under distilled water and then rinsed consecutively in 95% ethanol, xyline, and mounted with DPX mounting medium (sigma).

Image processing:

Stained samples were visualised using a LEICA DR2 bright field microscope under 10x, 20x, and 40x objective lenses and 10x ocular lens. Images were captured with a LEICA DC 500 digital camera. A standard stage micrometer was used to calibrate the optical images.

Image analysis and Measurement:

The eye diameter and mantle length were measured using digital callipers for specimens smaller than 10 mm ML and a standard ruler for larger specimens. Values were entered into a Microsoft Excel spreadsheet and a scatter-plot graph was constructed. The Data Analysis tool was used in the construction of the best fit regression line.

Retinal sections were analysed and measured using the calibrated ruler superimposed to the images at each magnification. The measurements were taken in central and peripheral areas of the retina, from the junction of the outer segment with the posterior chamber to end of the support cell layer. The measurements were repeated two more times per retinal section. Measurements were taken from an area representing equatorial retina.

Meta-analysis:

The meta-analysis utilised academic results from online science databases. Sources were included if they contained the name "*Teuthowenia*" in the text, and were then categorised by the predator, species of prey, and the greatest abundance of that species in the diet. Entries in which

the count was equal to one or the percentage in diet was less than 0.1 were excluded from the results.

Commonly Abbreviated Terminology:

ML—Mantle Length

MW—Mantle Width

HW—Head Width

BW—Funnel Base Width

FA—Funnel Aperture Width

LRL—Lower Rostral Length

1. Ontogenetic Development

Introduction:

Teuthowenia is a squid genus of the family Cranchiidae, whose largely transparent tissues have resulted in the common name 'glass' squids; their crypsis is also aided by eye photophores (Herring, Dilly & Cope, 2002), which counter-shade down-welling light from the surface (Young & Roper, 1977; Voss, 1985). Cranchiids have been reported from all oceans except the Arctic (Norman & Lu, 2000), and are found primarily between the mesopelagic and bathypelagic zones; however, some species, including those of the genus *Teuthowenia*, migrate vertically within the water column depending on maturity and seasonality (Voss, 1985; Moreno et al., 2009).

Teuthowenia presently contains three species (Voss, 1980; 1985): *T. maculata* and *T. megalops* are found in the central and northern Atlantic, and *T. pellucida* lives circum-globally in the southern sub-tropical belt (Voss, 1985).This widespread generic distribution, and the ability to migrate through the water column, indicates that these animals likely form components of several different oceanic trophic systems. However, relatively little has been reported about cranchiid predator–prey interactions in the deep sea, although beaks representing many genera—including *Teuthowenia*—have been found in the stomachs of top marine predators, ranging from seabirds (*e.g.*, Imber, 1992) to cetaceans (*e.g.*, MacLeod, Santos & Pierce, 2003).

Teuthowenia pellucida (Chun, 1910) has a complex systematic history. Since its original description by Chun in 1910, in which he attributed the species to the genus *Desmoteuthis*, it has been reported as part of eight different genera by different authors, and eventually placed within *Teuthowenia* by Voss (1980, 1985), who recognised its affinity with the other two known

members of the genus, *T. megalops* and *T. maculata*. All three species are characterised at maturity by their distinctive fin shape; large, eyes, each with three ventral photophores; and the presence of tubercles located externally at the two ventral fusion points between the head and mantle, placing the genus within the subfamily Taoniinae. However, characters for reliably identifying immature specimens are needed, especially during the larval stages, which bear morphological resemblance to several other genera.

The most appropriate terminology for immature cephalopods has been the subject of some discussion (Young & Harman, 1988; Sweeney et al., 1992). The term 'larvae' was disputed since most cephalopods have direct development (Young & Harman, 1988); however, Okutani (1987) described that, in contrast to octopods, "actively swimming oegopsid [squids] usually have a cylindrical or spindle-shaped muscular mantle in the adult phase, but a soft, saccular or dome-shaped mantle during juvenile stages," showing that squid do exhibit some morphological changes during maturation, which could be interpreted as metamorphosis. The term 'paralarval' was proposed, defined as post-hatchling cephalopods that display behavioural and/or morphological characters that differ from those of later ontogenetic phases, and pertain to their environment (Young & Harman, 1988; Sweeney et al., 1992; Hanlon & Messenger, 1996). As squid from several genera of Cranchiidae (*Teuthowenia, Helicocranchia, Sandalops, and Leachia*) have been shown to vertically migrate into deeper waters with maturity (Young, 1975; Young, 1978; Voss, 1985), young cranchiids were initially termed 'paralarvae' (Young & Harman, 1988); however, Sweeney et al. (1992) considered young cranchiids truly larval, indicating that some confusion remains. Both Young and Harman (1988) and Sweeney et al. (1992) agreed that after the post-hatchling phase, the squid should be considered a juvenile; for cranchiid squids, the juvenile phase begins when the eyes become sessile (Young & Harman,

1988). The sub-adult phase follows, defined by Young and Harman (1988) as a morphologically developed animal that still requires sexual maturation and/or further growth to reach adulthood. The present research uses the term 'larval' to refer to post-hatchling squid and aims to describe and illustrate the ontogenetic development of *T. pellucida* throughout the larval, juvenile, sub-adult, and adult phases, enabling reliable identification of individuals of all sizes.

Results:

A total of 109 specimens of *T. pellucida* were examined (Appendix 1), ranging in size from 1.5 to 210 mm dorsal mantle length (ML). The pre-adult stages were composed of 30 stage A, 4 Stage B, 3 Stage C, 9 Stage D, 15 Stage E, and 42 Stage F. Thirty of the specimens were adults, with 23 reproductively mature or mated. Previously reported maturity scales (Arkhipkin, 1992) for squid have focused on gonad development, with 'juvenile'/stage 0 encompassing all stages prior to visual sexual differentiation (Arkhipkin, 1992); however, young squids (particularly cranchiids) can also undergo significant morphological changes unrelated to sexual maturity. Documenting the progression of these stages is necessary to ensure correct identification of early life-stage specimens.

All phases of *Teuthowenia* possessed the head–mantle fusion characteristic of the cranchiids: one attachment site at the dorsal midline of the anterior mantle margin, and two ventrally, one on either side of the funnel. Other morphological characters were observed to develop through ontogeny (Fig. 1.1), with their progression characterising certain growth stages, as detailed below and outlined in Table 1.1. Some variation was observed in the sizes at which these developments occurred, so mantle length ranges given are approximate, and overlap for certain stages (especially Stages E and F).

Character / Developmental Stage	Mantle	Fins	Tubercles	Eyes	Eye Photophores	Arms	Tentacles
Stage A (Larva)	Saccular, 1–10 mm ML	Semi-circular	Absent	Pedunculate, contiguous with stalk	Absent	Short (less than 1 mm), about 3 suckers per arm	No defined club, suckers in proximal half in two series, distal half four series
Stage B (Larva)	Saccular, 10–20 mm ML	Paddle shaped	Absent	Pedunculate, contiguous with stalk	Absent	III=II=IV=I, Arms extend past buccal mass, ~20 suckers per arm	Tentacle tip pointed, no club definition, suckers in proximal half in two series, distal half four series
Stage C (Larva)	Tapered bell, 20–28 mm ML	Paddle shaped	1	Pedunculate, beginning differentiation	1 photophore	III=II>IV=I, 18–30 suckers per arm	Club defined with four series of suckers, stalk with two series in straight lines
Stage D (Juvenile)	Conical, 28–40 mm ML	Paddle shaped	2 or 3	Sessile, spherical	3 photophores (developing)	III>II>IV=I, 20–32 suckers per arm	Suckers on mid-manus expanded, rings visible*, zig-zag sucker pattern on stalk, sucker counts remain same
Stage E (Juvenile)	Conical, 40–70 mm ML	Paddle shaped	2–5	Sessile, spherical	All 3 photophores developed	III>II>IV=I, 22–32 suckers per arm	8–10 large teeth visible on sucker rings*, stalk similar; sucker counts remain same
Stage F (Sub-adult)	Conical, 45–100 mm ML	Ovular	2–5	Sessile, spherical	All 3 photophores developed	III>II>IV=I, 24–40 suckers per arm	10–12 large teeth visible on sucker rings*. Stalks similar. Sucker counts remain the same

Table 1.1—Key morphological characteristics of developmental stages in *Teuthowenia pellucida*. * under microscope at 40x magnification.

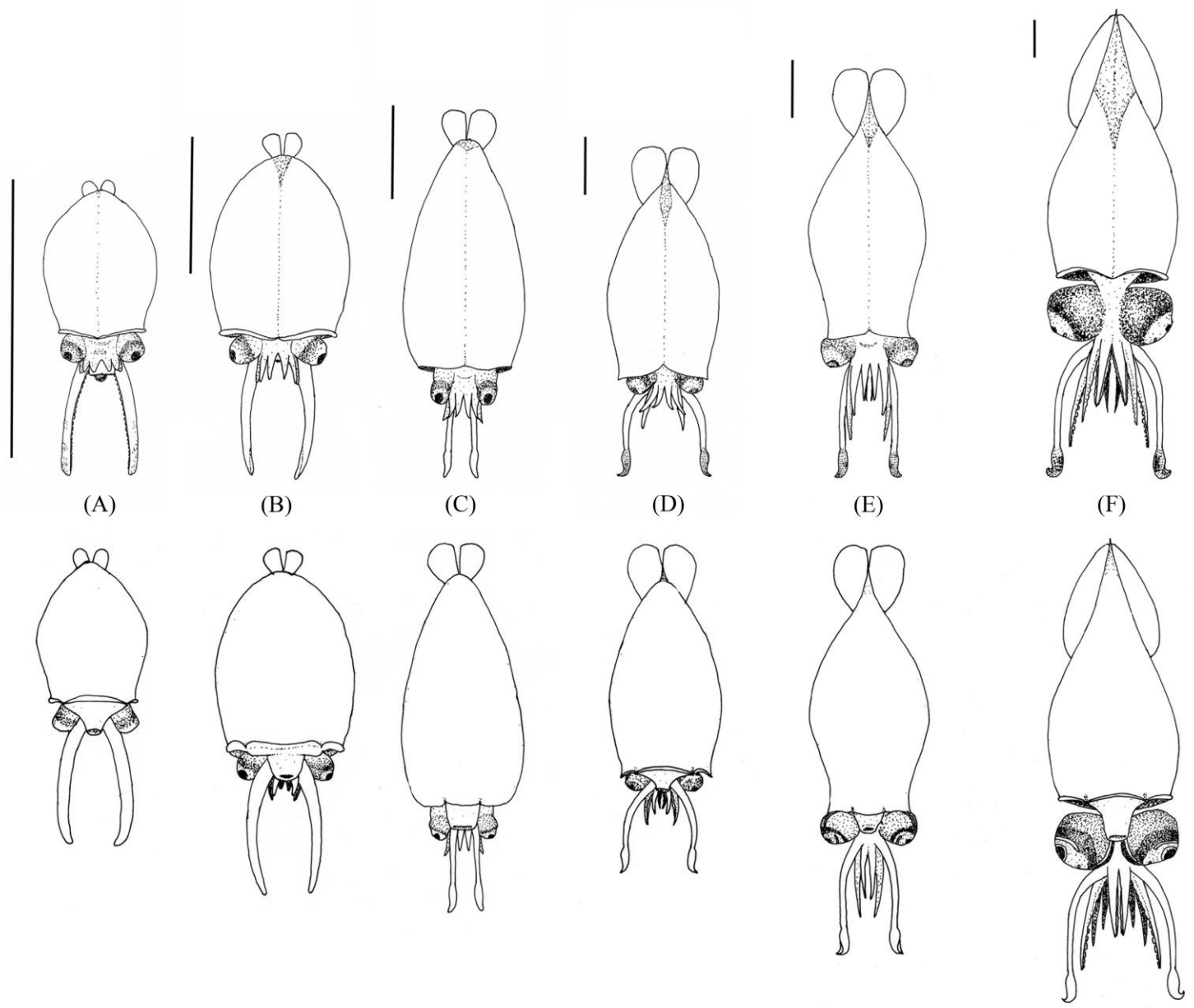

Fig. 1.1—Ontogenetic series of *Teuthowenia pellucida* showing both the dorsal (top line) and ventral (bottom line) view. Approximate mantle length range (A) 1–10 mm; (B) 10–20mm; (C) 20–28mm; (D) 28–40mm; (E) 40–70mm; (F) 45–100mm. Scale bar =1 cm.

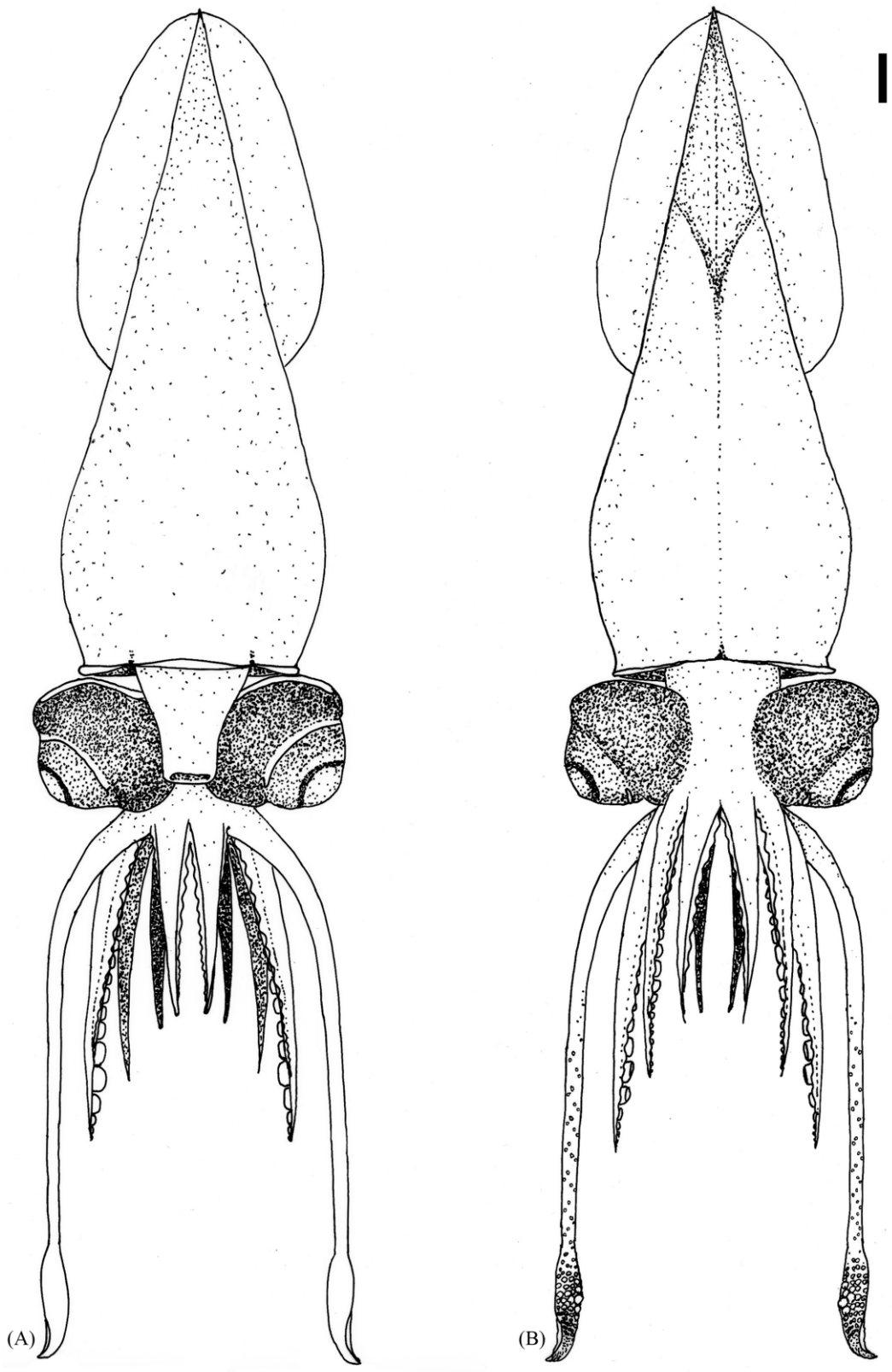

Fig. 1.2—Sub-mature adult *T. pellucida* (male, ML =135mm), (A) ventral and (B) dorsal view. Scale bar = 1 cm.

Pre-Adult stages (main characters summarised in Table 1.1).

Stage A (larval, ML ~1–10 mm; Figs 1.1A, 1.3A)—Mantle saccular; walls thin, gelatinous. Consistent localised patches of small, dark chromatophores (Fig. 1.4), about three to five per mm^2. Fins semi-circular, length and width <10% ML, ~99% of length posterior to mantle tip. Stalked eye length ~10% ML, eyes contiguous with stalk. Funnel widely conical, base ~70% total mantle width (MW), funnel aperture (FA) ~25% base width (BW). Gladius not visually continuous along dorsal midline. Arms stubby, less than 1 mm in length, not extending past buccal mass, each with dense cluster of small chromatophores on aboral surface and few suckers (four per arm at ML 5 mm). Tentacle length approximately equal to mantle length; stalks with several patches of small chromatophores on aboral surface in distal half;100–120 suckers present over each tentacle stalk and club: 12–20 present in two series on proximal portion of stalk, increasing to four series over distal portion and club (approximately 20 rows).

Stage B (larval, ML ~10–20 mm; Figs 1.1B, 1.3B)—Mantle saccular; walls thin, gelatinous. Gladius visible along entire length of midline, small conus visible just anterior to fins. Fins paddle shaped, length ~10–15% ML, width < 10% ML, ~99% of length posterior to mantle tip. Stalked eye length ~20% ML, eyes contiguous with stalk. Funnel conical, BW ~65% MW, FA~20% BW). Arms begin to extend past buccal mass; formula III=II=IV=I; arm length ~10–15% ML, each with about ten pairs of small suckers by end of stage, beginning at about 25% arm length and continuing to arm tip. Tentacles slightly shorter than ML; stalks thick, muscular, with small suckers along entire length, their numbers as in stage A. Tentacle narrows slightly at midpoint differentiating club from stalk, slightly concave along dorsal margin, tapering to distal point. Fleshy membrane forming along dorsal club margin. Club suckers enlarged towards centre, with diameter of largest twice that of tentacle stalk suckers.

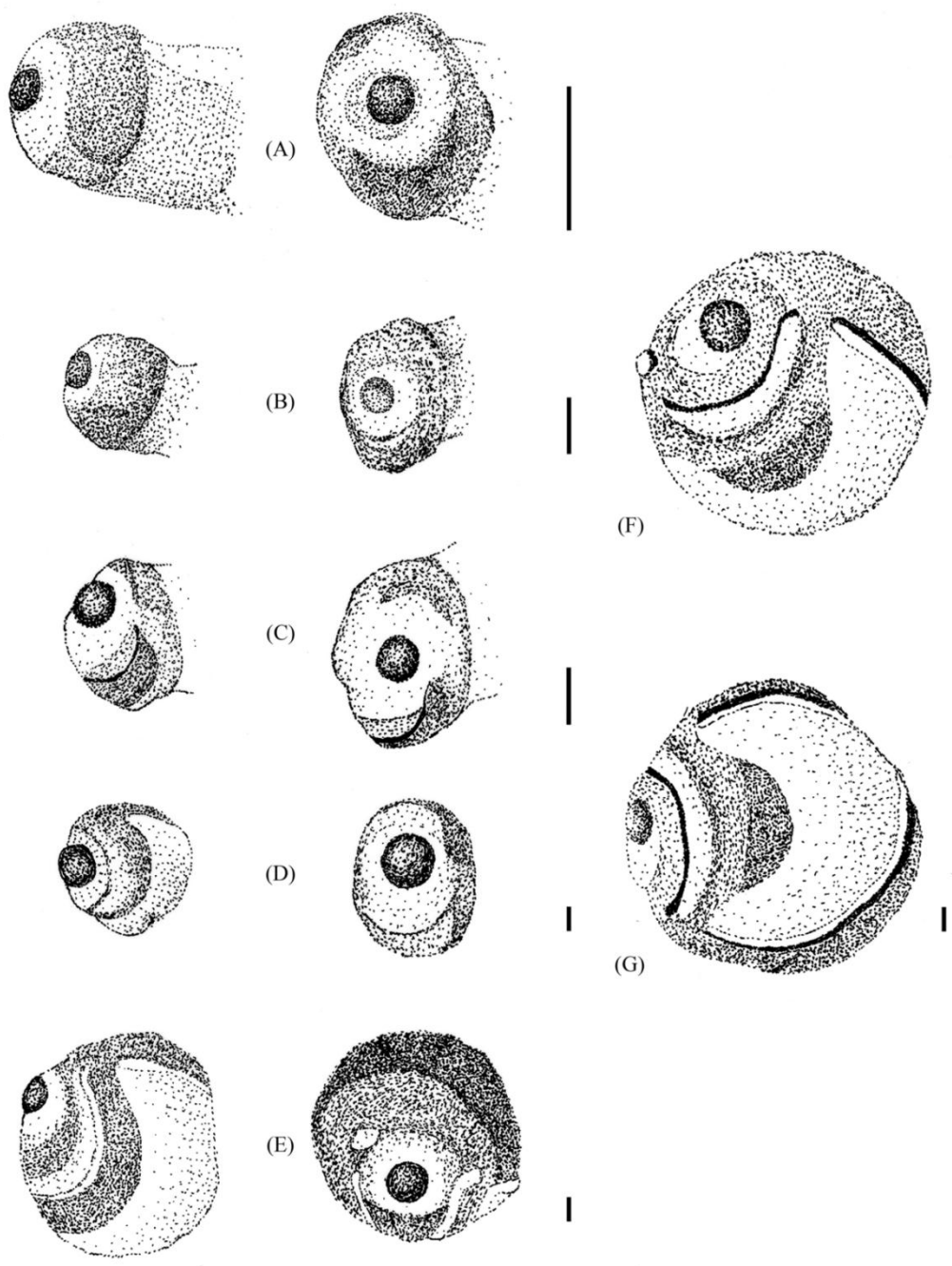

Fig. 1.3—Development of right eyes through ontogeny showing both anterior and lateral perspective. Eye presented from (A) stage A; (B) stage B; (C) stage C; (D) stage D; (E) stage E and F; (F) adult (anterior); (G) adult (ventral). Scale bar = 1 mm.

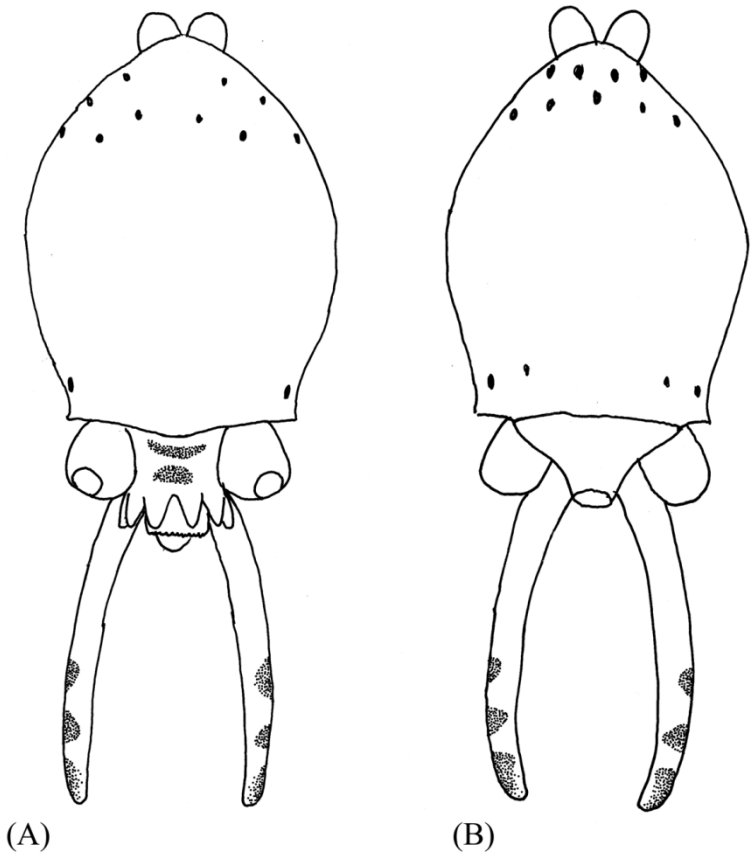

Fig. 1.4—Common chromatophore patterns on (A) dorsal and (B) ventral side of stage A larvae.

Stage C (larval, ML ~20–28 mm; Figs 1.1C, 1.3C)—Mantle proportionally larger than in earlier stages, tapering to blunt end. Fins paddle shaped, length ~10% ML, width ~15–20% ML, 95% of fin length posterior to mantle tip. Eyes on stout stalks, visually differentiated from stalk; first ventral photophore developing. Funnel as in Stage B, with single external tubercle present at each ventral mantle-funnel fusion point. Arms as in Stage B but with Arms II and III slightly longer; formula III=II>IV=I; Arms III 10–20% ML. Tentacle length <50% ML, club clearly differentiated; sucker counts and arrangement as in Stage B.

Stage D (juvenile, ML ~29–40 mm; Figs 1.1D, 1.3D)—Mantle conical; outer dermal layer with oval chromatophores, each <1 mm along long axis, sparsely spaced (about four per

cm^2). Fins paddle shaped, length and width ~30–35% ML; 40% of fin length posterior to mantle tip. Eyes spherical, stalks diminished, eye depth ~20% head width; all three ventral photophores developing. Head width approximately equal to mantle width. Funnel base ~50% MW, FA ~25% BW. Two or three tubercles on exterior mantle surface at funnel–mantle fusion points. Arms with 10–15 pairs of suckers each, formula III>II>IV≈I, Arms III 25–30% ML; oral face of arms bordered dorsally and ventrally by fleshy protective membrane. Tentacles ~50% ML; stalk with 12–20 pairs of suckers in zig-zag pattern along length (Fig. 1.5); club well defined, curves toward dorsal side distally, with fleshy membrane on both dorsal and ventral margins. Suckers enlarged mid-manus, with visible rings.

Stage E (juvenile, ML ~41–70 mm; Figs 1.1E, 1.3E)—Mantle conical, with similar chromatophore patterns as in previous stage. Fins paddle shaped, length 20–35% ML, width 13–15% ML; 20% of fins extend past mantle tip. Eyes bulbous, HW ~70–100% maximum MW, not stalked; all three ventral eye photophores fully developed. Funnel base ~25–30% MW, FA ~50% of BW. Arms with ~15 pairs of suckers each, formula III>II>IV=I, Arms III <30% ML; oral face of arms bordered dorsally and ventrally by fleshy protective membrane. Tentacles slender, length approximately 50% ML; club ~30% tentacle length, well defined, curving toward dorsal side distally, with dorsal membrane more pronounced than in previous stages. Approximately 80 suckers on club, largest in median two series at mid manus, with 8–10 large teeth visible.

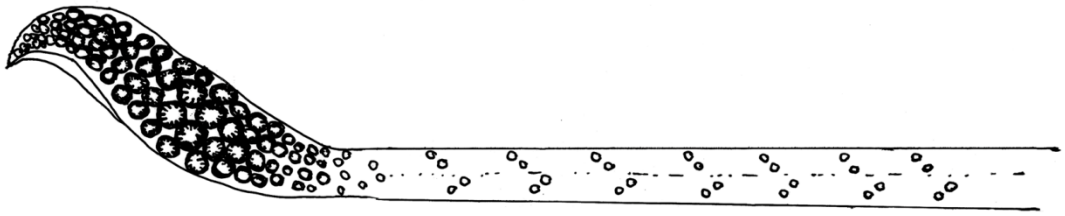

Fig. 1.5—Schematic diagram of left tentacle (from sub-adult) showing paired zig-zag sucker pattern on stalk.

Stage F (sub-adult, ML ~45–100 mm; Figs 1.1F, 1.3E)—Mantle conical; outer dermal layer with oval chromatophores, 1–2 mm at longest axis, sparse (five or six per cm^2). Fins thin, gelatinous, narrowly ovate in outline when taken together; length <50% ML, width 20–30% ML; not extending past mantle tip. Eyes large, causing head width to exceed mantle width; all three ventral photophores developed. Funnel conical, BW ~40–50% MW, FA ~50% BW; two to five tubercles present at funnel–mantle fusion points, mostly on external mantle surface but occasionally inside mantle cavity. Arms with 12–18 pairs of suckers each; formula III>II>IV=I, Arms III 30–50% ML; oral face of arms bordered dorsally and ventrally by fleshy protective membrane; largest suckers on distal half of Arms III. Tentacle length ~70–100% ML, with suckers as in Stage E; ~10–12 large teeth visible on sucker rings.

Adult (ML > 100 mm; Figs 1.2; 1.3F, G)

Mantle conical, maximum width (~40–50% ML) attained within anterior 20% ML; walls thin, gelatinous. Outer dermal layer with oval, reddish brown chromatophores, approximately 1–2 mm along long axis, 10–20 per cm^2. Gladius clearly visible along entire length of dorsal

midline (Fig. 1.2B). Conus visible over posterior 40–50% mantle length. Fins fleshy, ~50% ML, narrow (greatest width roughly equal to maximum mantle width), rounded at insertions, tapering to rounded point posteriorly. Two to five tubercles present at funnel–mantle fusion points (often several on external surface of mantle and one on fused area inside cavity; see Fig. 1.6). Funnel conical, BW ~30% MW, FA ~60% BW. Head width (measured from lens to lens) wider than maximum mantle width; outer surface of head covered with small, densely set chromatophores (about six per cm^2). Eyes (Fig. 1.3F, G,) large, oriented anterio-ventrally, each with three photophores (Figs 1.3F, G; 1.7): two large, crescent shaped (one around lens, one longitudinally ventral); one small, oval, at anterior periphery slightly above centre. Arm formula III>II>IV≥I, Arms III 30–50% ML; oral face of arms bordered dorsally and ventrally by fleshy protective membrane. Trabeculae on membranes align with pairs of suckers. Arms with ~15–20 pairs of adentate suckers; largest suckers present on Arms II and III; 4–6 enlarged suckers near tip about twice diameter of those at arm base. In mature males, distal 15% of Arms I and II modified, with four series of small suckers (Fig. 1.8B). In mature females, distal 15% of all arms comprised of fleshy, pigmented brachial organs (Fig. 1.8A). Tentacle length 80–100% ML; stalks thinner than bases of adjacent arms, narrowing toward clubs, with alternating pairs of small suckers (zigzag pattern) down length of stalk (Fig. 1.5). Clubs slightly expanded (Figs 1.2, 1.5), ~20% tentacle length, with fleshy dorsal and ventral membranes, the latter more pronounced; about 80 suckers present. Carpal area poorly defined, with suckers appearing randomly distributed proximally, then arranged in four series and increasing in size to mid manus, then quickly decreasing again distally. Suckers (Fig. 1.9) stalked, each with 24–30 teeth, longest distally.

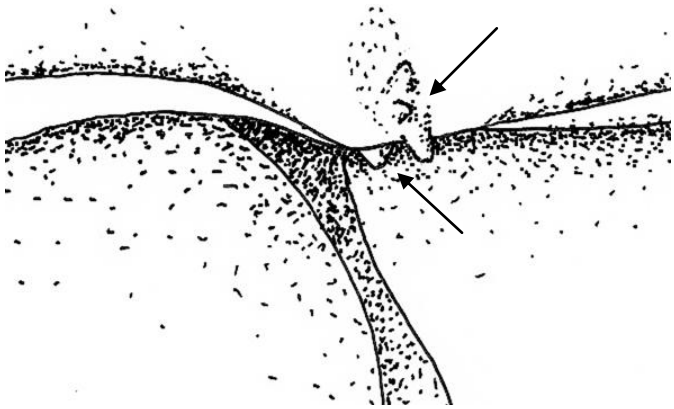

Fig. 1.6—Tubercles at the funnel–mantle fusion point (three on the exterior and one on the interior mantle surface indicated by arrows).

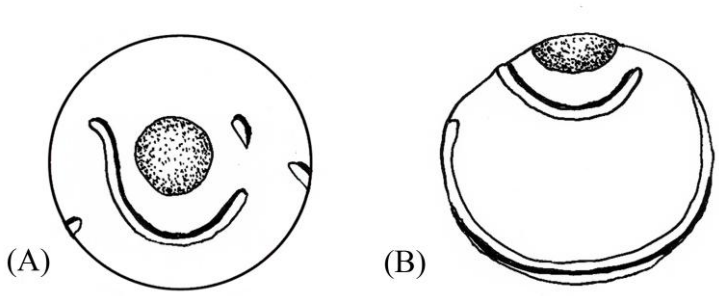

Fig. 1.7—Simplified diagram of eye photophores and lens from (A) anterior view and (B) ventral side of the eye.

Sexual modifications

Teuthowenia pellucida exhibits secondary sexual characteristics on the arms in both males and females. The suckers on the tips (distal ~15%) of Arms I and II in males increase from two to four densely set series (Fig. 1.8B). Females have distal brachial organs, consisting of two flaps of skin that overlap along the oral surface of all arms (Fig. 1.8A); these lack pigment during development, and darken to a deep red in mature specimens. This appearance is similar

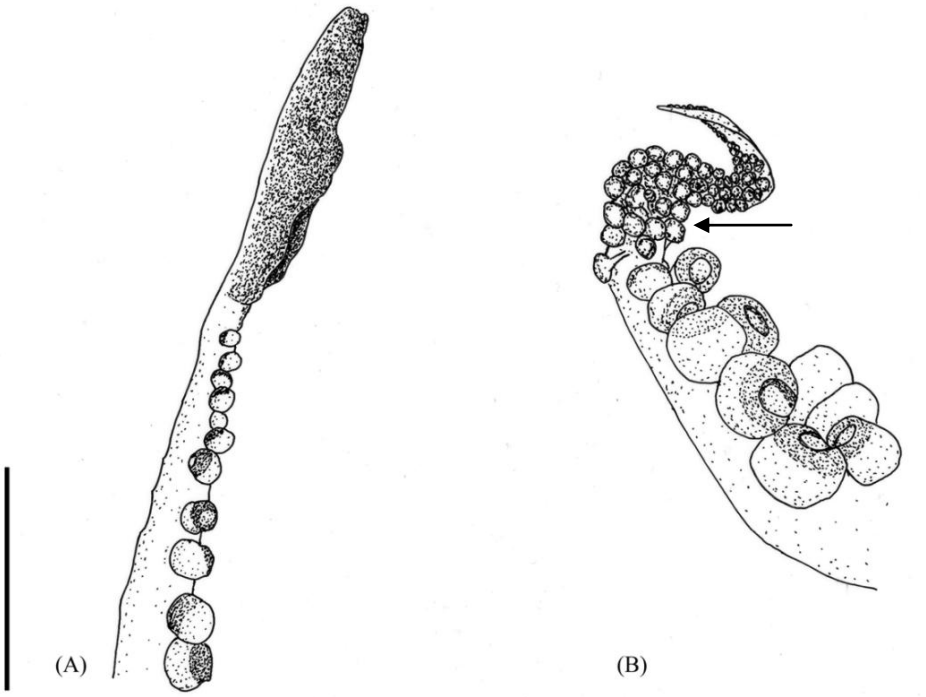

Fig. 1.8—Arm modifications in adult *T. pellucida*. Brachial end organ (A) on the tips of all arms in mature females; (B) four series of small suckers (indicated by arrow) on the tips of Arms I and II in adult males. Scale bar = 1 cm.

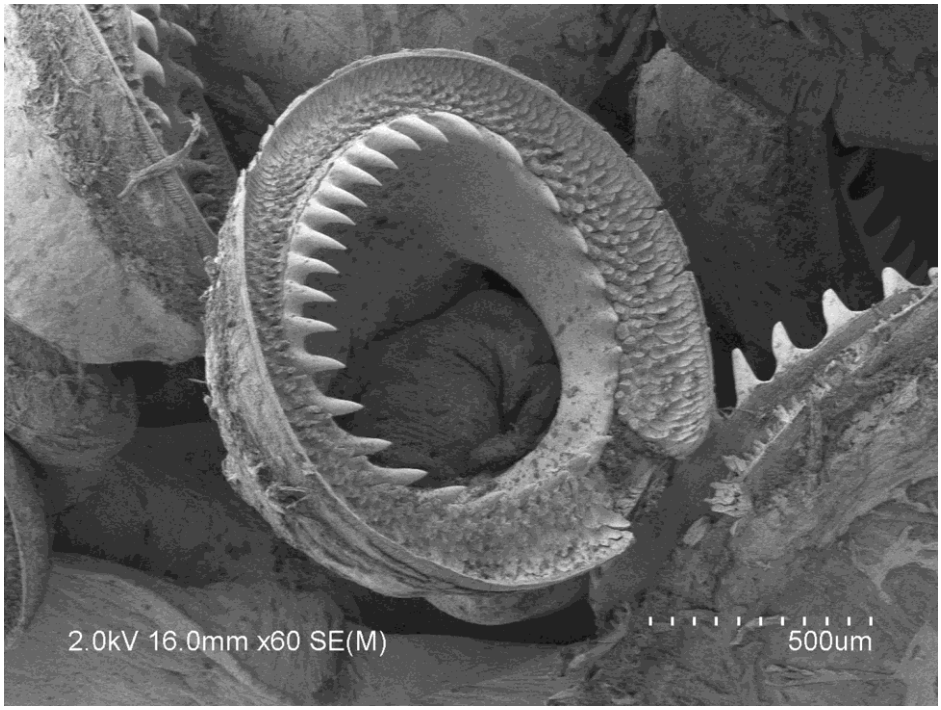

Fig. 1.9—Mid-manus tentacle club sucker ring showing 28 teeth.

among the six genera of cranchiids (*Cranchia*, *Liocranchia*, *Leachia*, *Teuthowenia*, *Megalocranchia*, and *Egea*) that display this feature (Herring, Dilly & Cope, 2002). Several examined females were reproductively mature, and three possessed large ovaries with near-mature eggs. The eggs were 1.6–2.8 mm along the longest axis, and an intact ovary was estimated to hold approximately 18,000 eggs. Nidamental glands from these three females were swollen and appeared to have encysted suckers attached to the outer membrane, as was previously documented by Voss (1980).

Internal Structures

Beaks (Fig. 1.10): Lower rostral length (LRL) of largest beak (adult male) 6.58 mm. Wings and lateral wall not fully darkened, 1–1.5 mm of clear surface area remained at periphery. In lateral profile (Fig. 1.10A, D, E), crest-to-base ratio 0.7; baseline length greater than height. Rostral tip slightly hooked, ending in sharp point. Jaw angle and wing angle both obtuse; rostral edge formed by two straight sections. Small rounded wing-fold covers jaw angle; wing-to-edge ratio 0.37. Hood and wings broad, narrowing at jaw angle. Wing fold appears un-thickened. Narrow ridge runs diagonally toward distal wing margin from shoulder. Hood moderately curved, shallow ridge running along wall of hood from rostral tip to hood edge; hood-to-edge ratio 1.39; hood just above crest. Crest narrow, not thickened, forming straight line in profile. Lateral wall with low ridge running horizontally, slightly above lateral wall mid-point. In ventral view, no indentation at hood edge midline or connection between lateral wall and crest. Free corners of lateral wall (along baseline) angled slightly outward.

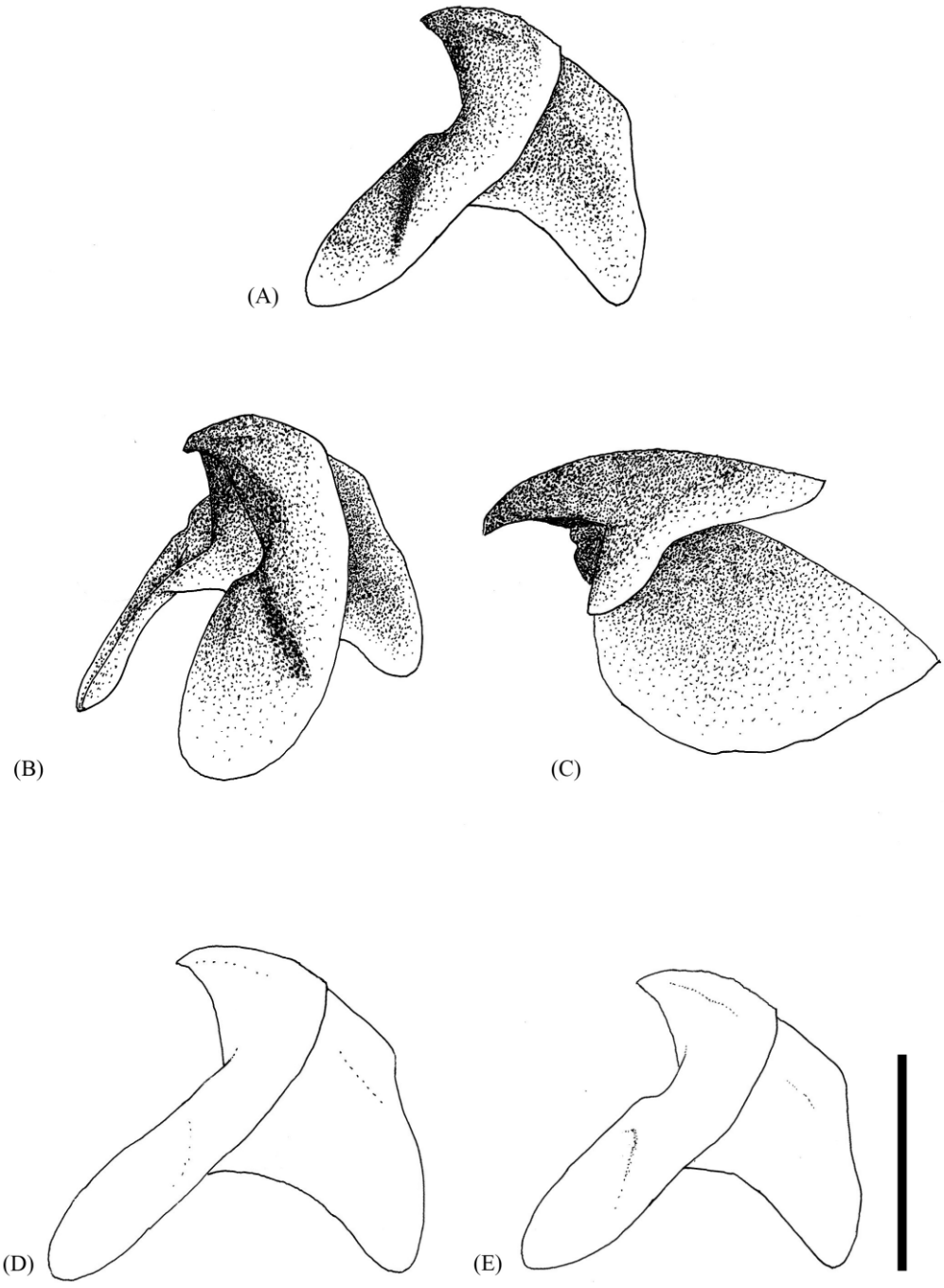

Fig. 1.10— Beaks of *T. pellucida.* (A, B, D, E) lower beak, lateral view except (B) oblique view; (C) upper beak, lateral view. (D, E) Phenotypic plasticity between beaks of similarly sized specimens (both males, ML ~150 mm). Scale bar = 1 cm.

Discussion:

Ontogenetic Development

In the most recent revision of the genus *Teuthowenia*, Voss (1985) summarised the larval stages of *T. pellucida* and *T. megalops*. However, the abundance of larval, juvenile, and sub-adult specimens of *T. pellucida* in New Zealand collections has permitted the present detailed investigations into the morphological development of this species through early ontogeny, resulting in the identification of seven developmental stages (whose key features are summarised in Table 1.1). As *Teuthowenia* larvae are often misidentified in collections or simply labelled 'cranchiid sp.,' it is hoped that the present findings will assist in the accurate identification of small specimens.

While examining larval *Teuthowenia*, it became apparent that certain body structures (*e.g.*, arm crown, eyes, mantle) do not develop uniformly, but rather undergo rapid changes during certain larval stages. For example, the mantle appears much larger relative to other body structures in larvae of Stage C than Stage B (Fig. 1.1), a result of the head and arms undergoing little absolute growth during this period, although structural changes are apparent. The eyes in Stage C, although still stalked, become more spherical in outline and the eye can be visually distinguished from the stalk itself. At this stage the larger crescent photophore is also developing on the ventral surface of the eye, the arm tips become pointed rather than blunt, and the tentacle club begins to differentiate from the stalk. Another dramatic change is observed between stages E and F (Fig. 1.1), where the fins change rapidly from the characteristic paddle shape seen in paralarvae to the approximately ovate juvenile/adult form. While several intermediate stages can be recognised during this change in shape (Fig. 1.11), they do not characterise separate larval

developmental stages, since the other morphological characters remain relatively constant. Since animals mature at slightly different rates, minor overlap was observed at the beginning and end of consecutive developmental stages; however, the transition between stages E and F had the greatest overlap, with the developments characterising Stage F beginning as early as 45 mm ML in some specimens and as late as 75 mm ML in others. It is between these sizes that juveniles begin ontogenetic descent into deeper waters (see Fig. 3.2).

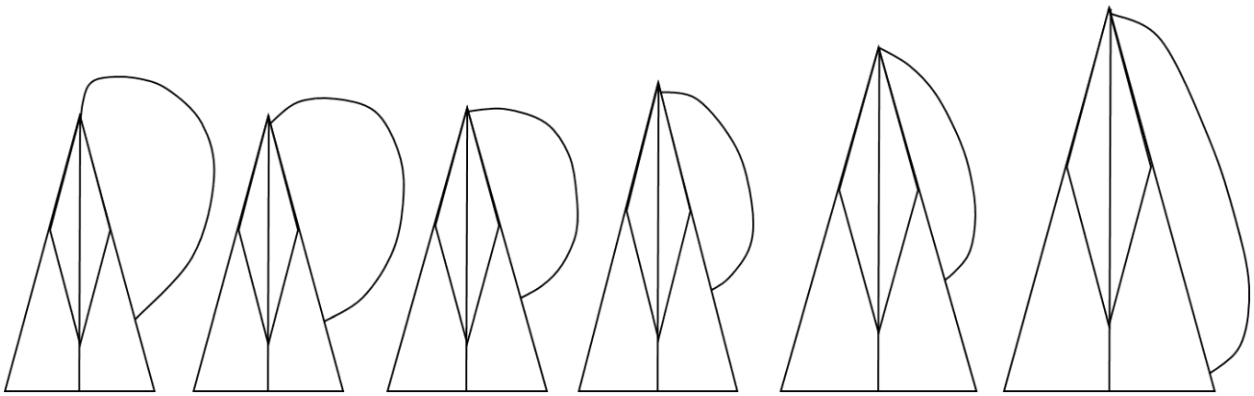

Fig. 1.11—Development of fin shape between juvenile and sub-adult phases (Stages E and F). Specimen maturation from left to right.

Recognition of these stages and their sometimes rapid transitions should make identifications of young *Teuthowenia* more reliable. Small individuals of other genera are often attributed to *Teuthowenia*, particularly if true *Teuthowenia* specimens of a given size are poorly represented in collections, precluding direct comparison. Much local confusion appears to occur in particular among *T. pellucida* at Stage C and similar-sized individuals of *Liguriella* and *Megalocranchia*, compounded by the relative scarcity of Stage C specimens (only three were identified during this study). However, at this size (ML 20–28mm), *Liguriella* and *Megalocranchia* each possess an elongated arm crown and eyes on long stalks (Fig. 1.12) with eyes narrowing ventrally in both genera, although this character is more noticeable in

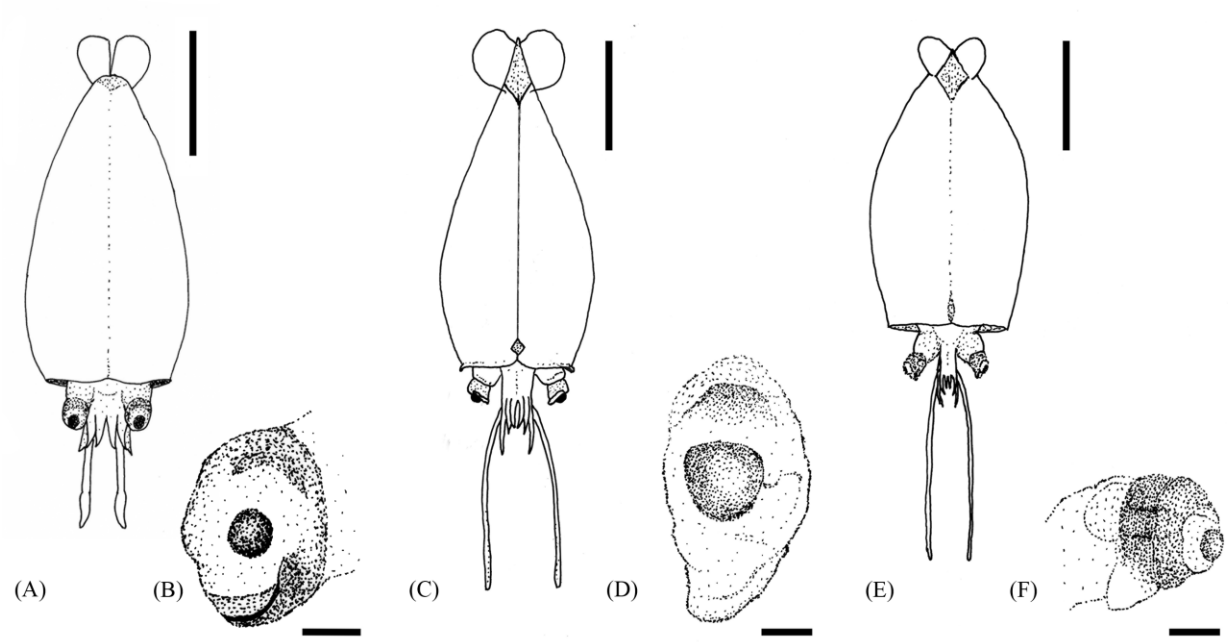

Fig. 1.12—*Teuthowenia* and other larval cranchiids, from New Zealand waters, with similar morphological characteristics. (A) *T. pellucida* (stage C) with enlarged diagram of (B) the eye viewed anteriorly, (C) *Megalocranchia* with enlarged diagram of (D) the eye viewed anteriorly, (E) *Liguriella* with enlarged diagram of (F) the eye viewed laterally. Vertical bar (A, C, E) = 1 cm, horizontal bar (B, D, F) = 1 mm.

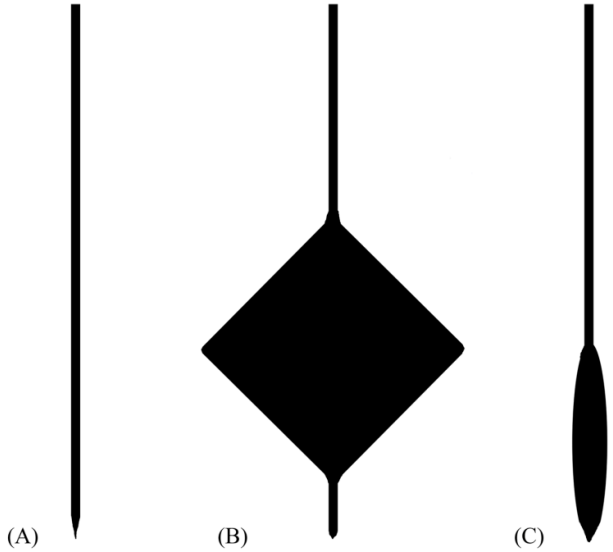

Fig. 1.13—Difference in visible rhachis shape at anterior dorsal midline of (A) *Teuthowenia*, (B) *Megalocranchia*, and (C) *Liguriella*.

Megalocranchia (Fig. 1.12B). Differences in the gladius visibility through the anterior part of the dorsal midline can also be observed: the rhachis in *Megalocranchia* can be seen through a very distinctive diamond-shaped translucent patch at the dorsal mantle fusion, while the same patch in *Liguriella* is distinctly oval, and in *T. pellucida* the area appears as a narrow point (Fig. 1.13).

Difficulties in differentiating these and other cranchiid genera at various life phases have historically complicated the family's systematics. While Voss (1980) considerably stabilised the Cranchiidae, by appraising the 41 nominal genera and rediagnosing the 13 genera considered valid today, much work is still required at the lower taxonomic levels. Although not within *Teuthowenia*, undescribed species are known to exist—*Liguriella*, *Egea* and several other cranchiid genera are believed to contain presently unnamed species (Voss, Stephen, & Dong, 1992)—and these can only be recognised where named taxa are well understood and described through as many life phases as possible.

Sexual Maturity

In mature individuals, apart from the coelom, the mantle lumen was dominated by reproductive tissues. Mating and spawning behaviours are largely undocumented for cranchiids; of the 13 genera, reproductive structures have only been completely described for *Teuthowenia pellucida* and *Galiteuthis antarcticus*, and this information is still largely speculative. Voss (1985) outlined the internal sexual structures of female *T. pellucida*, and the post-spawning anatomy of *Galiteuthis* was described by Laptikhovsky and Arkhipkin (2003). The temporal gap between the publication of these two studies, the fact that fecundity estimates from the present study are nearly three times higher than those previously reported for *T. pellucida*, and the fact

that size at sexual maturation has only been estimated in males to date (Voss, 1985), all indicate the need for further investigation into cranchiid reproduction.

One mature female contained approximately 18,000 eggs, which is a significant increase from the previous estimate of 6,000–8,000 reported for this species (Voss, 1985). However, this number is relatively low compared to some other species of squid; *Illex illecebrosus* can produce up to 400,000 ova (Durward, Amaratunga & O'Dor, 1979) and *Galiteuthis*, another cranchiid, is estimated to produce approximately 20,000 eggs (Nesis, Nigmatullin & Nikitina, 1998). Additional mature females should be examined if possible to assess the variability in fecundity within *T. pellucida*; for this study, the remaining mature females examined were slightly damaged, precluding accurate egg counts, although their ovaries appeared to have been similar in size to that of the intact specimen.

Secondary sexual features consisted of brachial end organs on all arm tips of females and modified arm tips on Arms I and II in males; in both sexes, suckers proximal to modifications did not change, as compared to sub-mature specimens lacking these sexual features. Some females lacked brachial organs due to damaged arm tips; this is consistent with results from Herring, Dilly, and Cope (2002), who found that all examined specimens of *Teuthowenia megalops* lacked all arm tips. Male arm modifications were more often retained, and most mature males exhibited the tight cluster of numerous suckers on the first two pairs of arms (Fig. 1.8B). Voss (1985) suggested that these modified arms could be used to caress the swollen nidamental glands in the female, with the suckers becoming encysted there; encysted suckers found on the nidamental glands of mature females examined herein support this theory. The function of sexual modifications in both males and females has not been confirmed; however, it is believed that the female's brachial organ may act as an attractant, either by emitting light

(Herring, Dilly, & Cope, 2002), by pheromone release (Voss 1985), or possibly a combination of both. Live observation of mating behaviours is needed to help confirm the function of these modifications.

Arkhipkin (1992) presented a scale for classifying cephalopod maturity based on reproductive features. Since all juveniles fall into his stage 0, there is little direct overlap between his findings and the presently identified larval stages (although it is possible that some currently unknown morphological character also indicates the onset of his stage 1). Both findings draw attention to the rapid growth and morphological changes that squid undergo during their early and late life stages, and serve as a reminder that, even for many species where the sub-adult and adult animals are reasonably well described, much remains to be observed about other phases of maturity.

Internal Structures

Some phenotypic plasticity was observed among the lower beaks, with all beaks falling along a morphological spectrum between those illustrated in Figure 1.10 D and E. In particular, differences were noted in relative (and absolute) wing and lateral wall length (both longer in Fig. 1.10D than E); wing width (narrower in Fig. 1.10D than E); and jaw and rostrum shape, with Fig. 1.10D having a proportionally longer LRL, and a more pronounced curve along the rostral edge, with a slight hook on the rostral tip (although this could have been due to the rostral tip being chipped off, a common occurrence). The shape of the wing fold also varied greatly, with some beaks (*e.g.*, Fig. 1.10E) possessing a more strongly curved shoulder at the wing fold, giving the appearance of an indentation at the jaw angle and more pronounced wing widening. In Fig. 1.10D, this indentation was not present, and the wing fold had a gentle curve into the wing. These variations occurred in many combinations, with some beaks differing from Fig. 1.10D or

E by a single character state, while others combined multiple characteristics of both. Additionally, and perhaps most importantly for beak–biomass calculations, the absolute LRL measurements of the two individuals illustrated in Fig. 1.10D and E—both males of ML ~150mm—differed, with D measuring 5.76 mm and E measuring 5.40 mm.

Initially, two possible explanations for this variation were considered: the maturity of the animal, and the possibility of sexual dimorphism. However, neither of these explanations appears to be correct as both animals appear to be at the same level of maturation, being reproductively mature adults at stage VI where spermatozoa have accumulated in the testis (Arkhipkin, 1992), and the ML of the individuals differs by one millimetre. Although several species of squid display sexual dimorphism within beak morphology (Bolstad, 2006; O'Shea, Jackson & Bolstad, 2007; Chen, Lu, Liu, Chen, Li & Jin, 2012), both of the beaks illustrated in Figs 1.10D and E were from males. When compared, beaks from males and females showed similar variations, indicating that neither variation was dominant in either sex. Beak E was inspected to see whether the indentation at the jaw angle was caused by damage during dissection; however, the shape of the indentation was rounded, with the edge appearing natural, not jagged as would be expected from recent (post-mortem) damage. Another possible explanation for the plasticity shown is water temperature during early development, as that is known to affect the growth of cephalopods (Leporati, Pecl & Semmens, 2007), it may also influence the shape of the beak. Although the proportions differ between beaks D and E (Figure 1.10), the features that distinguish them as *Teuthowenia* are very similar. Therefore, it was concluded that some of the beak features have a certain amount of intraspecific variation since no two beaks looked completely identical.

2. Retinal Structure

Introduction:

One of the most visually striking features of *Teuthowenia pellucida* is the large, bulbous eyes that make up the majority of the head. Many deep-sea vertebrates and invertebrates possess relatively large eyes, which maximise uptake of any light filtering down from the epipelagic zone (Land, 1981). Even in minimal-light environments, cephalopods rely on vision to interact with other members of the ecosystem; many of these interactions are over tens of meters, which in a low-light habitat are comparatively long distances (Sweeney, Haddock, & Johnsen, 2007). Cephalopods have a much more developed visual system than those of other molluscs, and have a similar ability to process complex images as vertebrates (Boyle & Rodhouse, 2005).

In squid, a spherical lens focuses the light onto a simple inverted retina. The eyes develop as invaginations of the skin midway through embryonic growth (Arnold, 1965). In myopsids, the eyes are protected by the cornea, which arises from tissue behind the eyeball and grows outward to cover the eye and lens (Arnold, 1984), Oegopsid squid eyes do not have this covering. The lens begins as a refractive rod, but develops into a sphere towards the end of development (Arnold, 1965). The lens is suspended in place by ciliary muscles, which are able to move the lens closer to the retina, in order to focus light (Boyle & Rodhouse, 2005). Projected light is inverted by the circular lens; therefore, the inferior retina processes down-welling light, while the superior retina processes upwelling light (Boyle & Rodhouse, 1965).

As in a vertebrate eye, the squid retina contains visual pigment, but most species are limited to a single pigment, retinal ($\lambda_{max} \approx 484$ nm). The firefly squid, *Watasenia scintillans*, is an exception in that it possesses two additional pigments: 3-dehydroretinal, with $\lambda_{max} \approx 500$ nm;

and a newly discovered pigment, 4-hydroxyretinal, with $\lambda_{max} \approx 470$ nm (Matsui, Seidou, Horiuchi, Uchiyama, & Kito, 1988; Seidou et al., 1990). Rhodopsin is a photosensitive chromoprotein with an attached retinaldehyde group (Hara & Hara, 1976). Retinaldehyde, also known as retinal, is the light-reactive component of the visual pigment in animals (Hyatt & Dowling, 1997). When light reaches the retina, the visual pigment is excited and triggers enzymatic reactions that signal the photic stimulation to the brain (Stryer & Bourne, 1986). Every type of pigment has a peak absorption at a narrow range of wavelengths, depending on the protein composition of the visual pigment; therefore, the protein present in the pigment determines the ranges of wavelengths that cause the most visual stimulation (Yokoyama, 1995). For many animals living in the deep sea, the peak absorbance of the pigment is between 470–480 nm, which is towards the blue end of the spectrum (Munz & McFarland, 1977). However, unlike a vertebrate eye, the pigmented portion of the photoreceptor is found on the inner surface of the retina (Boyle & Rodhouse, 2005), phasing the incoming light that directly stimulates it. In vertebrates, the inverted retina has photoreceptors in the deeper layers, and light passes through other cell layers before reaching the photoreceptors. Phylogeny, evolution, and space-saving designs have been proposed as reasons for vertebrates having inverted retinas over receiving incoming light directly (Duke-Elder, 1958).

Squid photoreceptors are long and slender, bundled together in groups called rhabdoms. The outermost segment of each rhabdom is composed of microvilli, which are extensions of the cellular membrane (Saibil & Hewatt, 1987). The rhabdom is in a parallel arrangement to other microvilli bundles, but at a perpendicular angle, in an orthogonal orientation in respect to the next rhabdom (Arnold, Summers, Gilbert, Manalis, Daw & Lasek, 1974). This allows for the detection of polarised light (Saidel, Lettvin, & Macnichol, 1983; Mäthger, Shashar, & Hanlon,

2009). The length of the photoreceptor is thought to correspond to its location in the retina (Matsui et al., 1988), as those found towards the ventral part of the retina tend to be longer than those found on the dorsal region. The same study concluded that longer photoreceptors were in a position to gather the most light, in this case, down-welling light; as the ventral photoreceptors would gather light from the surface.

The cellular structure of a coeloid cephalopod retina comprises three sections: the outer and inner photoreceptor and a darkly pigmented middle section that separates the two. The outer photoreceptor contains visual pigments that absorb incoming light, while the inner photoreceptor processes the signals and transmits them to the brain. The middle portion acts as a screen so that light does not enter the inner segment of the photoreceptor. The central screening pigment has been identified as ommin (Butenandt, 1959, as cited by Daw & Pearlman, 1974), and has been shown to migrate within the photoreceptor, depending on light conditions (Daw & Pearlman, 1974). This physiological characteristic acts as a screen to prevent over-stimulation of the photoreceptors.

Results:

Eye diameter and mantle length were compared to determine whether the eyes grow proportionally throughout ontogeny. The relationship between the diameter of the eye (0.5–33 mm) and the length of the mantle (1.5–165 mm) appears almost linear, but is in fact a power function; however, more data points from mature animals would strengthen this conclusion. In order to obtain a linear result, the natural log of the raw values was graphed (Fig. 2.1). The equation for the line of best fit is $y=0.057x - 0.878$ (R^2 value = 0.929).

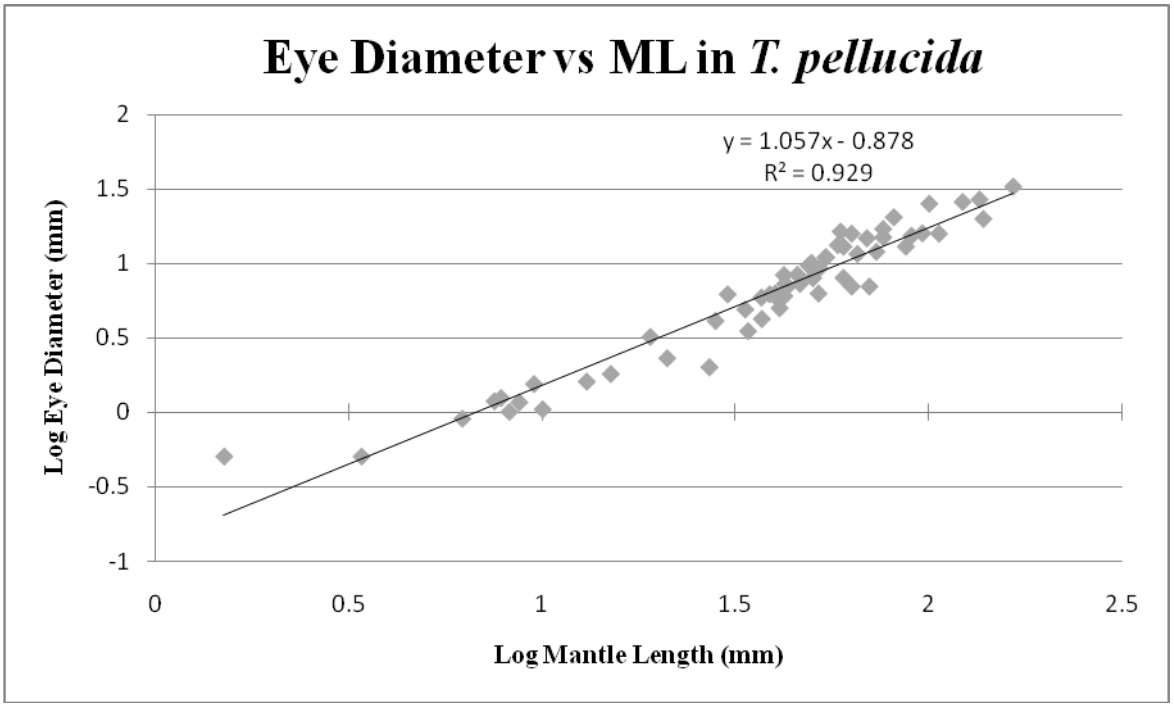

Fig. 2.1—Log relationship between mantle length (as an indicator of growth) and eyeball diameter.

After external measurements were recorded, the internal structure of the retina was examined. Retinal cross sections showed vertically striated cells in the outer portion of the photoreceptor; a thin, dark line (the screening pigment); and a darker-stained inner photoreceptor comprised of many oval cells (Fig. 2.2, 2.3). Table 2.1 shows measurements of the different retinal structures from specimens of ML 9.7–102.0 mm. Ratios comparing the lengths of the outer and inner segments were calculated; in younger specimens (*e.g.*, M.070961), the outer and inner segments are of nearly equal length, whereas the outer segment is relatively much longer in mature specimens (*e.g.*, 71673).

Table 2.1—Measurements (in micrometers) of photoreceptor components. The location refers to where the photoreceptors were found in the eye cup, either in the central portion of the retina (C) or peripherally, found closer to the lens (P). The outer photoreceptor segment (OS), ommin band, and inner photoreceptor segment (IS) make up the total photoreceptor length (total PR), which ranged from 75–380 µm. These values were added to the supporting cells to make the total retinal thickness (105–440 µm). Asterisk (*) indicates an approximation due to damaged layers.

Number	ML	Location	OS	Ommin Band	IS	Supporting Cells	PR	total retina	OS/IS	PR/ Retina
M.070961	9.7 mm	P	30	10	35	30	75	105	0.857	0.714
M.070961	9.7 mm	C	50	10	40	50	100	150	1.250	0.667
M.287201	27.0 mm	P	110	5	70	65	185	250	1.571	0.740
M.287201	27.0 mm	C	75	5	70	70	150	220	1.071	0.682
NIWA 71673	50.0 mm	P	130	10	15	45	155	200	8.667	0.775
NIWA 71673	50.0 mm	C	190	10	20	60	220	280	9.500	0.786
M.074310	52.0 mm	P	220	10	10	60	240	300	22.000	0.800
M.074310	52.0 mm	C	220	10	15	80	245	325	14.667	0.754
M.067262	52.0 mm	P	185	10*	20	20	205	225	9.250	0.911
M.067262	52.0 mm	C	290	10*	35	100	325	425	8.286	0.765
NIWA 71673	102.0 mm	C	360	10	10	60	380	440	36.000	0.864
NIWA 71691	128.0 mm	P	290	10	25	50	325	375	11.600	0.866
NIWA 71691	128.0 mm	C	340	10	30	50	380	430	11.333	0.884

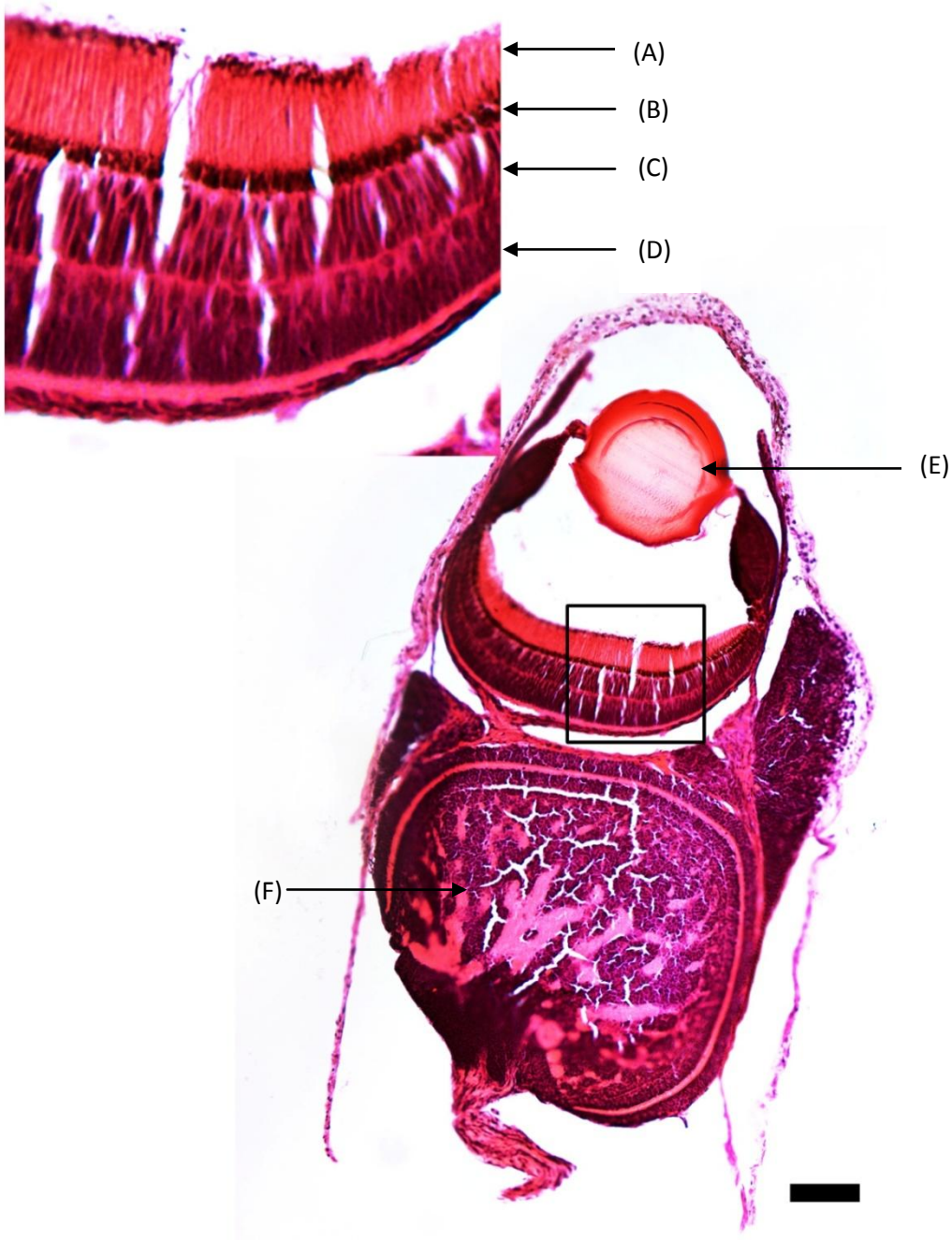

Fig. 2.2—Cross-section of larval (Stage A) *T. pellucida* eyeball, with expanded retinal area showing the (A) outer photoreceptor, (B) ommin layer, (C) inner photoreceptor, (D) supporting cells, (E) lens, and (F) the optic lobe of the brain (NMNZ M.070961, ML 9.7 mm, bar equals 100 µm).

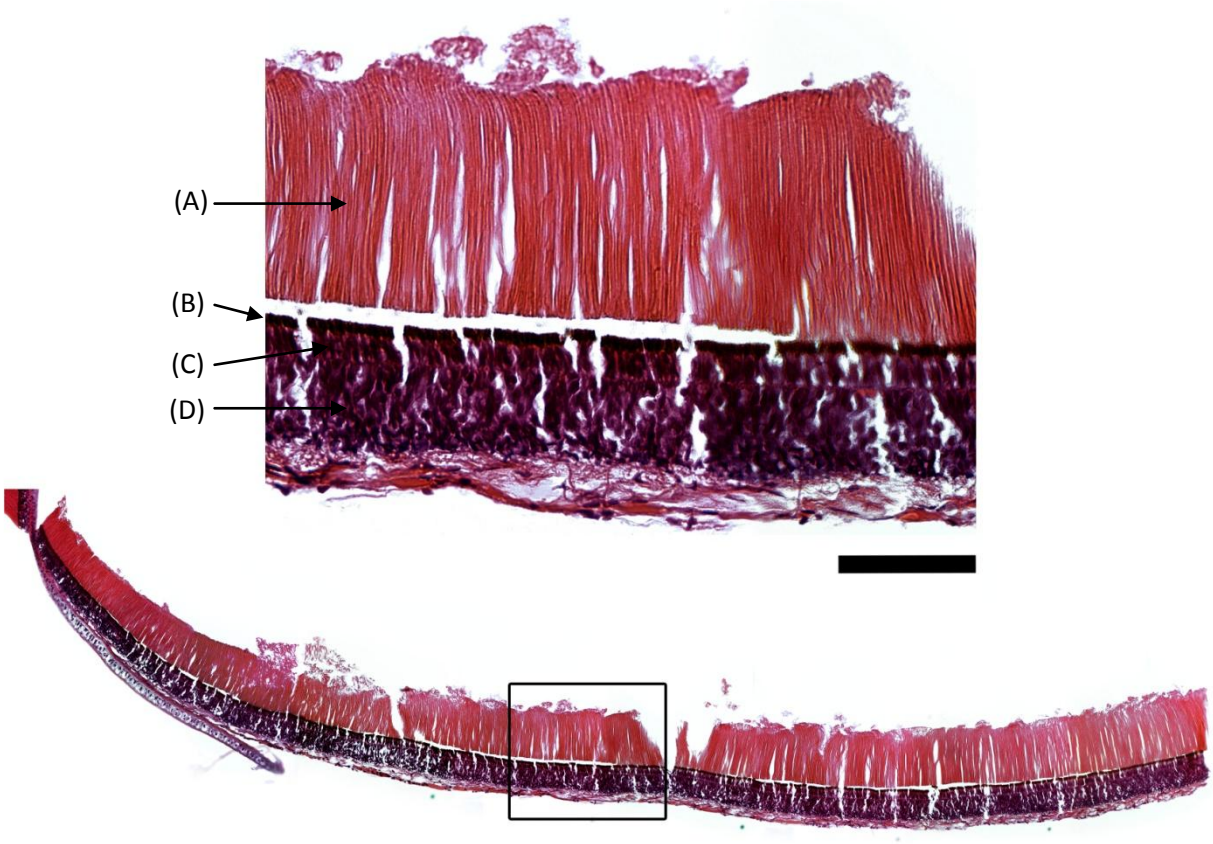

Fig. 2.3 —Cross section of the retina of sub-mature adult *T. pellucida* (bottom) with enlargement (top). Enlarged section shows the (A) outer segment, (B) ommin layer, (C) inner segment and (D) supporting cells. (NIWA 71673, bar equals 100 µm)

The outer segments of several retinas deviated from the standard retinal structure found in most cross-sections. Several of the retinas examined were not structured in the usual parallel arrangement of cephalopod photoreceptors; instead, they appeared to 'fan' or flare outwards as they approached the outer surface of the retina (Fig. 2.4). This pattern started midway through the outer segment, with the outer ends of the rhabdoms expanded out to 10–20 times their basal diameter. Another outer segment displayed two coloured bands when stained (Fig. 2.5). Although the presence of multiple outer-segment bands has been shown previously in *Watasenia scintillans*, it has never been documented in *Teuthowenia*. Only one specimen displayed this staining pattern.

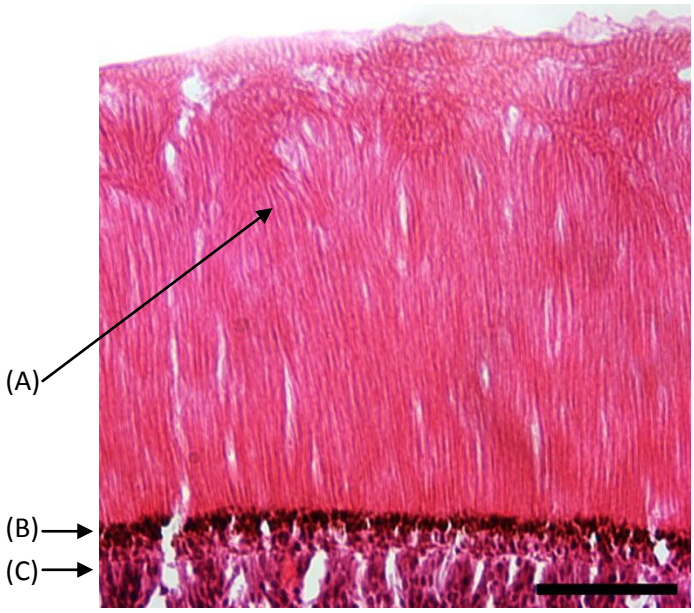

Fig. 2.4—Cross section showing central photoreceptor ‘fanning’ pattern in (A) outer segment. (B) ommin layer, (C) inner segment. (NIWA 71673, ML 102 mm; bar equals 100 µm).

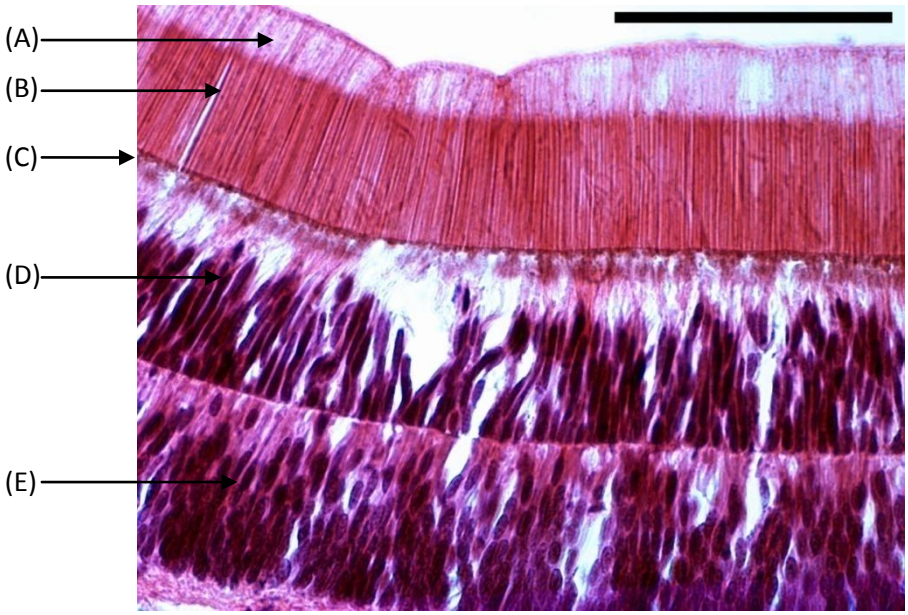

Fig. 2.5—Cross section showing both (A) a light and (B) dark stained band in the central outer segment of the photoreceptor. (C) Ommin layer, (D) inner segment and (E) supporting cells appear similar to other specimens of comparable size. (NMNZ M.287201, ML 27 mm, bar equals 100 µm).

In larval and juvenile specimens, an ommin layer was observed between the inner and outer segment, and a migrated ommin layer (which moved within the photoreceptor cell) was also present at the outer end of the photoreceptor (Fig. 2.2). The migrated ommin was more abundant in the central area of the photoreceptor, while the peripheral area had little migrated ommin. In sub-adult and adult specimens, ommin positions varied. In some specimens, the ommin had not migrated at all, and in others it was sparsely scattered amidst the outer segment of the photoreceptor. One retina had a sparse scattering in the central area of the photoreceptor and a denser migrated ommin layer at the peripheral photoreceptors (Fig. 2.6), indicating that the periphery of the retina had received more photic stimulation than the central retina.

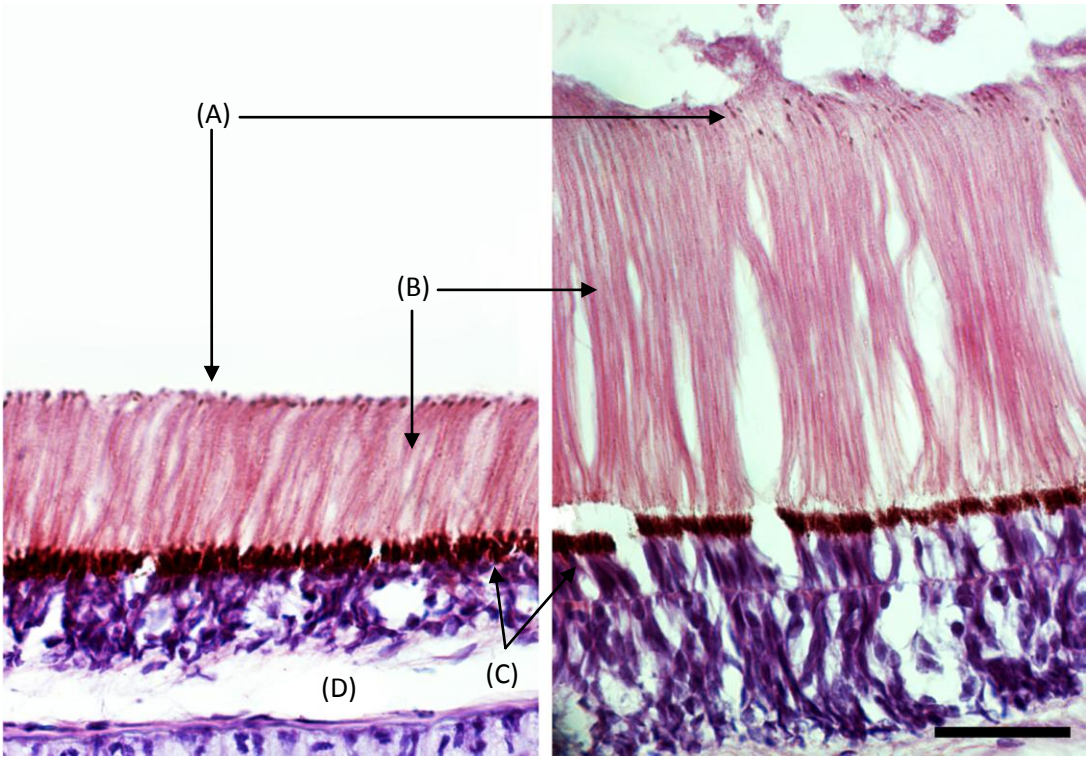

Fig. 2.6—Distribution of the migrated ommin layer (A) in the peripheral (left) and central (right) portions of the outer segment (B) of the retina of a sub-adult. (C) Main ommin layer and (D) inner segment also shown. (NIWA 71673 ML 50.0 mm, bar equals 100 µm).

Discussion:

Many animals that rely on vision in the deep sea have proportionally large eyes; the cephalopod orders Teuthida and Vampyromorpha are excellent examples. The vampire squid, *Vampyroteuthis infernalis*, has the largest eye-to-body ratio of any animal, with the diameter of the eyes being about one sixth the total length of the animal (Johnson, 2000). The largest eyeballs in the animal kingdom belong to the giant squid (*Architeuthis dux*) and the colossal squid (*Mesonychoteuthis hamiltoni*), and can be up to 10 inches in diameter (Roper & Boss, 1982; Nilsson, Warrant, Johnsen, Hanlon, & Shashar, 2012). However, these large eyes are proportionate to the body sizes of the animals, which can be up to 13 m and possibly 6 meters, respectively (Bolstad, 2003). Little is known about the visual capabilities of deep-sea cephalopods because their tissues are often gelatinous and fragile, and severely damaged or destroyed entirely during capture (Sweeney, Haddock & Johnsen, 2007). *Teuthowenia* is no exception; its eyes are particularly large (making the head width sometimes greater than the mantle width) and were often badly damaged on the material examined herein. These large eyes seem disproportionate to the size of the body; however, observations of eye diameter throughout ontogeny suggest a fairly constant ratio to mantle length (Fig. 2.1). However, this conclusion would be better supported with addition of intact adult specimens.

The relationship between eye size and mantle size in *Teuthowenia pellucida* was non-linear, but the curve was shallow. Voss (1985) reported that *Teuthowenia,* like other cranchiid squids, undergoes an ontogenetic vertical migration. As larval and juvenile members of the species reside at shallower depths, the eyes would be subjected to much higher light intensities. However, larger eyes would be more beneficial as the animal matures and descends into the deeper waters. Therefore, it would be expected that the curve would be more noticeable, as

younger animals do not have as much need for proportionally large eyes. Since the relationship between eye and mantle size was nearly linear, it could be hypothesised that visual abilities are equally important for larval organisms as they are in adults. The large eyes, found in many deep-sea species, are used to gather as much light as possible, both down-welling from the surface and bioluminescent signals from other deep-sea animals (Collin & Partridge, 1996). Thus, in addition to the increased size of the eye during maturation, the retina should be optimised to collecting the minimal amounts light found in this dark environment through the lengthening of photoreceptors. At around 50 mm ML, the eye diameter–mantle length ratio begins to show more variability, with values becoming less tightly correlated. This increased variation in ratio occurs at a similar size as *T. pellucida* begins ontogenetic descent into deeper water (see Fig. 3.2); this suggests a possible connection between eye size and photic habitat.

Although the cellular composition of the photoreceptor does not change with maturity, a change was observed in the proportions in the inner and outer photoreceptor lengths. In early development, a nearly equal ratio was found between the lengths of the outer and inner photoreceptors (Fig. 2.2). In most instances, the length of the outer photoreceptor was much longer than the inner photoreceptor during adulthood, comprising 89–97% of the total photoreceptor length (Table 2.1). Hypothetically, ontogenetic vertical migration could be caused by the development of the eyes, and the lengthening of the photoreceptors; if older organisms have longer photoreceptors, the retina would have an increased sensitivity to light, therefore causing the squid to move into deeper areas of the ocean where less photic stimulation would occur.

Central photoreceptors were commonly longer than photoreceptors found peripherally. This was consistent with the findings of Matsui et al. (1988), who showed that the length of the

photoreceptor increases in areas where the most light would contact the retina. In this case, the longer outer segments found centrally would indicate that the retinal area directly behind the lens was structured to gather the most incoming light. It is also possible that the increase in length of this part of the photoreceptor was due simply to the age of the animal, as older animals, in general, had significantly longer outer photoreceptor segments. If age is the reason for this increase, further investigation is needed to explain why the inner and outer segments do not grow at a proportional rate.

The photoreceptors of squid eyes are long, thin filaments that normally form straight bundles (rhabdoms). However, in several specimens examined, the normally cylindrical bundles instead flared out in the outer segment (Fig. 2.4). No reference to any similar pattern could be found in reports of any other animal's photoreceptors to date. The difference in structure of the outer segment could be due to damage to the photoreceptor during the hemisecting process, as the outer tip of the photoreceptor can sometimes appear 'fanned'. If that were the case, the pattern should not be found in cross-sections taken further within the tissue; however, the pattern seems to be consistent in retinal sections throughout these particular eyes. It is possible that the photoreceptors are flared outwards in order to present more surface area to capture incoming light; however, further testing would be required before any such conclusion could be drawn.

It appears from these results that, unlike inner and outer photoreceptors, the screening layer of ommin (found between them) does not change in absolute thickness with growth of the specimen. In most samples, this layer remained approximately 10μm; however, in one instance the layer was damaged, and the approximate thickness was determined using fragmented portions of the photoreceptor. This suggests that the same amount of ommin sufficiently protects the longer photoreceptors of older animals, as there is less of a requirement for ommin as the

animal matures. Daw and Pearlman (1974) showed movement of this ommin layer in the squid *Loligo pealei*. When introduced to high-light conditions, some of the ommin migrated from the screening layer up to the outer edge of the photoreceptor over the course of 5–15 minutes. This shift was believed to occur in order to prevent over-stimulating the receptors. Daw and Pearlman (1974) found that ommin had the same absorbance as rhodopsin, therefore acting as a screen that shielded the inner receptors from excess incoming light. After the light source was removed, the ommin began to return to the screening layer within several minutes (Daw & Pearlman, 1974).

Similar migrations appear to happen in the eyes of *Teuthowenia*, as all smaller specimens had a darkly pigmented 'layer' at the tip of the outer receptor (Fig. 2.2). This dark area became less abundant or non-existent in more mature specimens. Since larval *Teuthowenia* have been shown to live between 0 and 200 meters, while older animals are more often encountered from deep, aphotic waters (Fig. 3.2; Voss, 1985), their retinas would receive far more light. However, once the adults move into the deep-sea pelagic zones, if eyesight remains important to the animal's survival, then the structure of the eyes should be configured to gather the most light possible; this explains why the outer photoreceptor segment is significantly longer in older specimens. An interesting exception was one sub-adult specimen that showed little ommin present in the central outer segments of the photoreceptors, where it was expected to be located based on other examined material; instead, the migrated layer was present along the periphery of the retina (Fig. 2.6). This pattern was not consistent throughout cross-sections of the entire eye, indicating that these may have been localised patches of ommin. The peripheral ommin layer shown in Figure 2.6 could indicate an ability to focus where light is absorbed, as the central, longer photoreceptors would absorb more light. This localised ommin migration could also have occurred during capture of the specimen. Daw and Pearlman (1974) found that if more than 10%

of rhodopsin is isomerised, the migrated ommin layer does not return to the base of the outer segment. This research did not take into consideration the length of the photoreceptor; therefore, it is possible that the rhodopsin is isomerised in shorter photoreceptors before the longer ones. More research is required to determine whether the length of the photoreceptor affects the rate of overstimulation.

The eye from M.287201 (ML 27 mm, Stage C) had several interesting differences from other specimens. The proportions between the outer and inner segments of the photoreceptor were nearly equal at the peripheral portion of the retina; these proportions are similar to those seen in Stage A larval specimens. It was also the only specimen in which the photoreceptor cells in the peripheral portion of the retina were longer than those in the central portion (110 µm versus 75 µm). This could indicate that those photoreceptors were receiving the most light, as was shown in Matsui et al. (1988), or that there was an error during the dissection, making the cross section on an angle. However, larval Stage C is characterised by several changes in eye morphology (the eye shape becomes more spherical, the stalks shorten, and the first photophores begin to form—see Chapter 1). It is therefore possible that changes in the retinal structure also take place during this larval stage, with the outer photoreceptor beginning to lengthen.

The retinas of most squid species contain only one photopigment, limiting the eyes' peak sensitivity to a certain range of wavelengths (Seidou et al., 1990). However, the photoreceptors of the firefly squid, *Watasenia scintillans*, have three photopigments, and can therefore absorb light at several wavelengths (Matsui et al., 1988). These different photopigments were indicated by three different coloured bands which were visible after the staining process. These bands appeared very similar to those seen in the retina of one specimen herein (Fig. 2.5); however, the staining processes used in each instance were not the same. The examined photoreceptors

showed both a light pink stained section and a dark pink stained section in the outer photoreceptor. This staining pattern was not seen in retinal sections from any other specimens. Therefore, several explanations exist: this is possibly a unique individual which shows two photopigments in the outer photoreceptor, instead of just one. Alternatively, the multiple stained bands indicate there was some error or artefact from the staining process; however, given the ubiquitous presence of both colours along the entire length of the retina, this appears to not be the case. Chemical tests should be included in future work on the eye in order to confirm whether there are multiple pigments present in the retinal tissue. Multiple pigments would enable the animal to be able to detect a wider range of wavelengths, improving its visual capabilities.

Another interesting result from the research herein, was the presence of a cornea-like membrane covering the lens of larval specimens (Fig. 2.2). As stated previously, no cornea is known to cover the lens of oegopsid squids. However, it appears that *Teuthowenia pellucida* hatchlings have a protective membrane over their eyes that disappears as they age, as the membrane was absent by the time the eyes became sessile (between Stages C and D). Further research should investigate the development of this membrane, whether it appears on hatchings of other oegopsid squid species, and if it serves to further protect the retina of the hatchling from excess light.

Conclusion:

Teuthowenia pellucida inhabits different photic zones during different life phases. The juvenile members of this species commonly reside in the epipelagic zone, while adults vertically migrate down into the aphotic zone. Given that this animal lives in several habitats, this

research notes morphological changes within the retinal structures that may coincide with vertical migration. In *Teuthowenia pellucida*, the photoreceptors increase in length as the animal matures, which enables the retina to collect more light in a darker environment. Thus, both the size of the eyes and the length of the photoreceptor cells found in the retina of deep-sea species appear to improve their visual abilities. However, there appears to be a lack of knowledge when comparing the visual abilities of cephalopods. To confirm these results, the eye growth of a continually epipelagic or bathypelagic species should be compared to those of *Teuthowenia* to determine whether the herein observed eye development is unique to species that migrate deeper with ontogenetic development.

3. Trophic Importance

Introduction:

In addition to its systematics, understanding a species' ecological role is important wherever possible. Assessing trophic interactions can provide insight into an animal's physical or behavioural attributes, as well as its distribution and sometimes even phylogeny. However, most of the marine ecosystems studied to date have been coastal, epipelagic, and benthic ecosystems, while the ecology of the pelagic deep sea remains largely unstudied (Webb, Vanden Berghe, & O'Dor, 2010). Webb et al. (2010) showed that more than 50 percent of global marine diversity records were from areas that constituted less than 10 percent of the total ocean volume. This showed a significant under-representation of marine diversity in mid- and deep water habitats.

Squid make up the majority of the pelagic cephalopod fauna, and can comprise a large portion of the diets of many marine vertebrates, ranging from seabirds to whales (*e.g.*, Imber, 1992; Beatson, 2007). Several squid species are targeted by large global fisheries and are commercially profitable. However, species that are not targeted are still caught as bycatch, especially in finfish and crustacean fisheries, impacting marine trophic dynamics in both well-researched and poorly studied marine ecosystems (Olson, Román-Verdesoto, & Macias-Pita, 2006). Unfortunately, a large majority of these bycatch squid species are largely unstudied, as they have no commercial value, and are part of the meso- or bathypelagic ecosystems, making them more challenging to observe. For some non-commercial squid species, like *Taningia danae*, global distributions are thought to be relatively well understood, although abundance data remain scarce; for others, even geographic ranges remain incompletely known.

For marine organisms, abundance can be calculated using live specimens that are visually recorded, by trawl catches, or estimated using the remains of dead animals. Cephalopod remains are often obtained from the stomach contents of larger predators, particularly cetaceans, seals and seabirds. For instance, using this method, it has been estimated that Antarctic seal and bird populations can consume a combined total of around 260,000 tonnes of squid a year (Guinet, Cherel, Ridoux & Jouventin, 1996). These calculations are made primarily using cephalopod beaks (see Fig. 1.10), which are one of the few hard structures in these animals, have species-specific morphology, and are retained in the stomach longer than other tissues; they are therefore often used to calculate prey biomass and composition. The structure of squid beaks (one upper and one lower) consist of the hood, lateral walls, and the rostrum (the curved tip of the beaks that make up the jaw), with the lower beak also having wings that connect to the hood (Xavier & Cherel, 2009). The rostral edge of the lower beak is usually measured (lower rostral length, LRL) and used as the basis for biomass calculations. Many beaks have unique morphological characteristics that differentiate them from other species; however, these differences can be subtle, and make identification challenging. Descriptive beak guides aid in the identification of these features (*e.g*., Clarke, 1986; Xavier & Cherel, 2009). The beaks can also be used to estimate the size of the animal based on allometric beak regression equations, most commonly equating mantle length to LRL.

Xavier and Cherel (2009) described the beaks of members of the family Cranchiidae as having a "wide range of characteristics and most beaks can be confused with other families". The beak of *Teuthowenia pellucida* is similar in appearance to that of another cranchiid, *Galiteuthis glacialis;* however, it differs in having a fold in the lateral wall, and a proportionally smaller crest (Xavier & Cherel, 2009). *Teuthowenia pellucida* is not thought to be a common

prey item in the Southern Hemisphere (Xavier & Cherel, 2009); however, *T. megalops* (which is distributed throughout the North Atlantic) appears to be a common food item for some species of whales and dolphins (Fordyce, Mattlin, & Wilson, 1979; Santos, Pierce, Herman, Lopez, Guerra, Mente, & Clarke, 2001a; Santos, Pierce, Smeenk, Addink, Kinze, Tougaard, & Herman, 2001b). Given the trophic importance of another species of *Teuthowenia*, it is therefore possible that the importance of *T. pellucida* as a food item in Southern Hemisphere trophic systems is underestimated. To gain insight into the three known *Teuthowenia* species' role as prey, a review of published reports of *Teuthowenia* as prey follows.

As mentioned previously, many deep-sea ecosystems are not well understood and that lack of knowledge could negatively affect species from other ecosystems. Deep-sea cephalopod species show higher levels of pollutants in their tissues than those living in surface waters (Froescheis, Looser, Cailliet, Jarman, & Ballschmiter, 2000). Anthropogenic pollutants found in tissues of deep-sea cephalopods living at 1000 m depth, *Teuthowenia* included, can also accumulate in the tissues of their predators (Unger, Harvey, Vadas, &Vecchione, 2008). The threat of anthropogenic pollutants in the deep sea and the impact on the organisms there is a recently discovered issue with no known solution. This shows a need for understanding both deep-sea trophic systems and environmental factors that affect them.

Results:

Specimens examined were from mid-water and bottom trawls, and indicated that *Teuthowenia pellucida* is ubiquitous around New Zealand (Fig. 3.1). The vertical range of trawls ranged from the surface down to 1439 meters (Fig. 3.2); however, locality and size data were not available for all specimens. Figure 3.2 also shows a general trend of ontogenetic descent:

specimens below 50 mm ML were only caught above 200 meters, as were most between 50 and 100 mm ML, while adults (those specimens above 100 mm ML) were found at depths greater than 200 meters. This is consistent with vertical distributions described by Voss (1985).

Trophic relationships

Cranchiid squids are found in most tropical and temperate oceans, and are accordingly preyed upon by a wide range of predators. While a number of reports exist of *Teuthowenia* as a prey species (Table 3.1), its trophic role is far from comprehensively understood, since nothing is known of its own predatory role: there are no reports of dietary findings for any *Teuthowenia* species. Nor were any gut contents encountered in any specimen examined in this study. Transparent cephalopods are believed to have rapid digestion, minimising the amount of time digested material would compromise the crypsis of the animal (H. J. Hoving, personal communication, May 9, 2013). The viscera in *T. pellucida*, like those of most cranchiids, occupy a relatively small volume within the mantle, and many individual organs (apart from the reproductive structures in mature specimens) were difficult to discern even in the largest individuals.

Future investigation into the diets of these animals may be possible using molecular techniques (although some gut contents would still be necessary for sampling), or more general trophic information could be gleaned from stable isotope work.

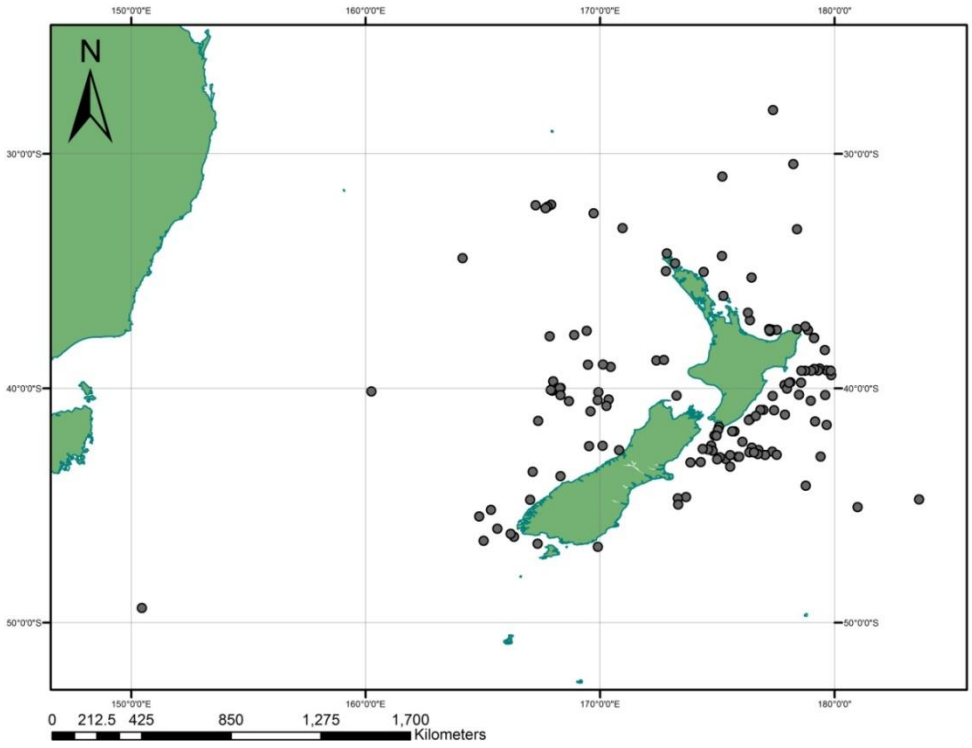

Fig. 3.1—Distribution of *Teuthowenia pellucida* around New Zealand (n=145).

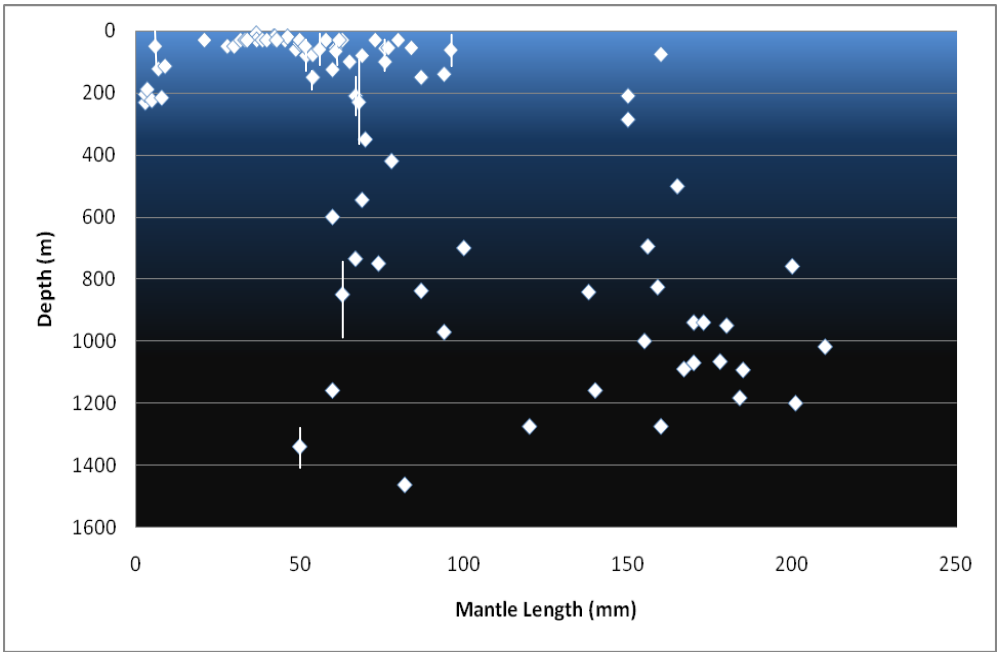

Fig. 3.2—Vertical distribution of *Teuthowenia pellucida* (n=87). Lines indicate a depth range of capture.

Table 3.1—Predators of *Teuthowenia.* Under "Proportion of prey", N = total number of beaks found in the stomach contents, W = estimated percentage of total tissue weight consumed, O = frequency of occurrence in examined individuals.

Predator	**Species**	**Proportion of Prey**	**Source**
Birds			
Cory's shearwater (*Calonectris diomedea*)	sp.	10 (1.4% N)	Neves, Nolf & Clarke, 2012
Providence petrel (*Pterodroma solandri*)	*pellucida*	13 (2.4% N)	Bester, Priddel & Klomp, 2010
Rockhopper penguin (*Eudyptes chrysocome*)	*pellucida*	3.2% N	Tremblay & Cherel, 2003
Rockhopper penguin (*Eudyptes chrysocome*)	sp.	"common"	Bourne, 1986
Sooty albatross (*Phoebe triafusca*)	sp.	53.7% N	Green, Kerry, Disney & Clarke, 1998
Southern buller's albatross (*Diomedea bulleri*)	*pellucida*	2–5 (<0.5% W)	James & Stahl, 2000
Wandering albatross (*Diomedea exulans*)	*pellucida*	0.16–1.35 % W	Imber, 1992
Wandering albatross (*Diomedea exulans*)	*pellucida*	6 (0.8% N)	Cooper, Henley & Klages, 1992
Cetaceans			
Cuvier's beaked whale (*Ziphius cavirostris*)	*megalops*	16.23% N	Santos et al., 2001b
Cuvier's beaked whale (*Ziphius cavirostris*)	*megalops*	25.3% W	Santos et al., 2001b
Cuvier's beaked whale (*Ziphius cavirostris*)	*megalops*	41.2% W	Santos et al., 2001b
Cuvier's beaked whale (*Ziphius cavirostris*)	*megalops*	45.7% N	Fordyce et al., 1979
Cuvier's beaked whale (*Ziphius cavirostris*)	sp.	8% N	Sekiguchi, 1994
Layard's beaked whale (*Mesoplodon layardii*)	*pellucida*	18.3% W	Sekiguchi et al., 1996
Long-finned pilot whale (*Globicephala malaena*)	*'megalops'*	10.8% N	Clarke & Goodall, 1994
Long-finned pilot whale (*Globicephala melas*)	*pellucida*	2 (2.1 % N)	Beatson & O'Shea, 2007
Northern bottlenosed whale (*Hyperoodon ampullatus*)	*megalops*	17.3% W	Santos et al., 2001a
Northern bottlenosed whale (*Hyperoodon ampullatus*)	*megalops*	"common"	Santos et al., 2001c
Northern bottlenosed whale (*Hyperoodon ampullatus*)	*megalops*	"important"	Santos & Pierce, 2005

Table 3.1—continued

Predator	Species	Proportion of Prey	Source
Northern bottlenosed whale (*Hyperoodon ampullatus*)	sp.	223 (17% N)	Hooker, Iverson, Ostrom & Smith, 2001
Pygmy sperm whale (*Kogia breviceps*)	*pellucida*	18% W	Beatson, 2007
Pygmy sperm whale (*Kogia breviceps*)	sp.	0.8 % W	Wang, Walker, Shao & Chou, 2002
Short-beaked common dolphin (*Delphinus delphis*)	*megalops*	17 % O	Lahaye et al., 2005
Short-beaked common dolphin (*Delphinus delphis*)	*megalops*	38 (0.3% N)	Brophy, Murphy & Rogan, 2009
Short-beaked Common dolphin (*Delphinus delphis*)	*megalops*	68.8% O	Pusineri, Meynier, Hassani & Ridoux, 2007
Sperm whale (*Physeter macrocephalus*)	*maculata*	1.8 % N	Clarke, Martins & Pascoe, 1993
Sperm whale (*Physeter macrocephalus*)	*megalops*	0.34 % W	Santos et al., 1999
Sperm whale (*Physeter macrocephalus*)	*megalops*	3.5 % N	Clarke, Martins & Pascoe, 1993
Sperm whale (*Physeter macrocephalus*)	*pellucida*	1.8% N	Evans & Hindell, 2004
Sperm whale (*Physeter macrocephalus*)	*pellucida*	0.63 % N	Clarke & Roper, 1998
Striped dolphin (*Stenella coeruleoalba*)	*megalops*	1099 (10.9% N)	Ringelstein, Pusineri, Hassani, Meynier, Nicolas & Ridoux, 2006
True's beaked whale (*Mesoplodon mirus*)	sp.	50% N	Sekiguchi, 1994
Fish			
Blue shark (*Prionace glauca*)	*megalops*	2 (0.9% N)	Clarke, Clarke, Martins & De Silva, 1996

Discussion:

Distribution

The geographic and vertical distributions of *T. pellucida* examined herein (Figs 3.1 and 3.2) agree with previous reports (Voss, 1985). The vertical distribution of this species was generalised based on trawl data, which were limited in some cases by lack of detail in the collection records. With more detail, such as the time of trawling, this research could support the belief that *Teuthowenia* display diel (as well as ontogenetic) vertical migration, as was previously concluded by Voss (1985), and would explain the range of depths at which specimens over 50 mm ML were captured. Several of the trawl records indicated that individuals were recovered from the stomach contents of deep-sea fish. Two of the specimens examined herein were retrieved from the stomach contents of hoki (*Macruronus novaezelandiae*) and orange roughy (*Hoplostethus atlanticus*); both are commercially fished in New Zealand waters.

Predation on Teuthowenia

Although *Teuthowenia pellucida* is not believed to play a strong overall role as prey in southern-hemisphere trophic systems (Xavier & Cherel, 2009), it is an important regional source of food for several species of whales (Table 3.1). Beatson (2007) showed that over 18% of the stomach contents in beached remains of the pygmy sperm whale (*Kogia breviceps*) were beaks from *T. pellucida*, making this the third-most important prey species for this whale. Similarly, in the gut contents of Layard's beaked whale (*Mesoplodon layardii*) *T. pellucida* was estimated to have made up 18.3% of mass consumed (Sekiguchi, Klages & Best, 1996). Although *M.*

layardii was shown to feed on *Teuthowenia* throughout the southern hemisphere, its greatest consumption of *T. pellucida* was around New Zealand.

Overall, the trophic role of *Teuthowenia* appears much better studied in the northern hemisphere, particularly the Atlantic Ocean. *Teuthowenia megalops*, which lives in the North Atlantic, makes up a large part of the diets of several marine predators. Both Santos et al. (2001b) and Fordyce, Mattlin, and Wilson (1979) showed that *T. megalops* comprises 40–46% of the diet of *Ziphius cavirostris* by examining stranded specimens. Species such as the common dolphin, *Delphinus delphis*, also consume *T. megalops*, but as a much lower proportion of the diet (although beaks from *T. megalops* were found in nearly 70% of the stomachs). This indicates that, while they do not rely on this species as a primary source of food, it is still commonly eaten, and not just a random catch. Interestingly, *T. maculata* only appeared in the diets of one study (Clarke, Martins & Pascoe, 1993). This could be due to a lack of study in the central Atlantic, or the erroneous identification of beaks from this species.

Several types of seabirds have also been shown to consume species of *Teuthowenia*. These range from penguins (*e.g.*, Trembley & Cherel, 2003), to shearwaters (*e.g.*, Neves, Nolf, & Clarke, 2012) and albatrosses (*e.g.*, James and Stahl, 2000; Imber, 1992; Cooper, Henley, & Klages, 1992; Green, Kerry, Disney, & Clarke, 1998). In most cases, *Teuthowenia* does not make up a large part of these birds' diet; however, Green et al. (1998) documented that over 50% of the diet of the Heard Island sooty albatross population is comprised of *Teuthowenia*. This was determined by looking at the regurgitations and casts of both adults and chicks. While it may initially seem odd that deep-sea species are preyed upon in such great numbers by seabirds, there are several possible explanations. Firstly, as many cranchiids (including *Teuthowenia*) have been shown to migrate vertically during development (Voss, 1985), juveniles dwelling in

epipelagic waters could be preyed upon by seabirds; however, this seems unlikely as several studies reported beaks from adult *Teuthowenia* in the diets of seabirds (Hedd & Gales, 2001; Neves, Nolf & Clarke, 2012). Secondly, spent adults (those that have spawned) could float up to the surface after death, as was observed for two spent *Galiteuthis* specimens under the surface of the ice in Antarctic waters (Nesis, Nigmatullin & Nikitina, 1998). If the gelatinous, spent bodies of other cranchiids also rose to the surface regularly, it is possible that scavenging birds could feed on them. Thirdly, seabirds could scavenge beaks from the bycatch or gut contents thrown into the ocean from fishery vessels, as some fisheries gut their catches at sea (Thompson, 2008) and most discard their non-target species immediately. Finally, birds may be scavenging pieces of tissue and beaks from the stomach regurgitations of marine mammals. Whales regularly extrude the beaks collecting in their stomachs through either excretion or regurgitation (Santos & Pierce, 2005). Clarke, Croxall and Prince (1981) suggested that seabirds such as albatross scavenge tissue from odontocete regurgitate, as results showed that some of the squid represented by beaks in the stomach contents would have been too large or lived too deep for the bird to hunt them.

One potentially important factor when considering the predation of *Teuthowenia* is seasonality. Clarke et al. (1993) showed that the abundance of *Teuthowenia* in the diet of the sperm whale (*Physeter macrocephalus*) found off the Azores changes depending on the time of year. In April, they found 365 beaks belonging to *T. megalops* in the stomach of one whale; however, from September to December, this number dropped to below 50 in each of the eight stomachs examined. At this point in the year, beaks from *T. maculata*, which had not been present for most of the year, increased. Since *T. maculata* is found in the East Atlantic, off the coast of Africa, Clarke et al. (1993) concluded that this showed evidence of migratory patterns in

sperm whales. This is an important aspect to consider as many large marine mammals migrate throughout the year, and their diets probably change accordingly. Within the same region, cephalopod species may also be more abundant at certain times of the year. For instance, it is possible that spent adult squid are abundant in the diets of marine mammals during and after the squids' spawning season, but would not be present at other times during the year.

Another important factor to consider when examining the diets of marine predators is the developmental phase of the prey they are eating. Larger prey provides a higher caloric reward to the predator. Santos (2001a) showed that the estimated capture size of *Teuthowenia megalops* by bottlenose whales (*Hyperoodon ampullatus*) was 75–285 mm ML. As *T. megalops* matures at a larger size (around 260 mm ML) than *T. pellucida* (Voss, 1985), several developmental phases could therefore be encompassed in the diets of predators. Since *T. pellucida* matures at a smaller size, around 100–150 mm ML, any predator that hunts for a similar size range of prey than that mentioned in Santos (2001a) would potentially consume fewer larval specimens of *T. pellucida* than of *T. megalops*. It is therefore important to consider that smaller predators, which would be feeding on juvenile and larval phases of *Teuthowenia,* could have stomach contents composed primarily of larval beaks. Most beak identification guides focus on mature (or near-mature) individuals; therefore, knowledge on the occurrence of earlier life phases in diets is lacking. In many cases, the digestive juices most likely erode away most of the beak itself in smaller individuals, making the beak difficult to identify and providing a possible under-representation of immature squid in the diets of marine predators, both large and small.

The health of a predator may also play a role in the proportion (if any) of deep-sea squid in its diet. While strandings can occur due to disorientation in healthy animals, they may also indicate health problems (Dawson & Slooten, 1990). An unwell animal may be eating less,

and/or may not be able to dive to its usual foraging depths. In one study (Sekiguchi et al., 2010), fewer stomach contents were recovered from stranded than non-stranded dolphins and in stranded dolphins of most species studied, cephalopods comprised a lower proportion of the total prey. The number of cephalopod prey species differed greatly: non-stranded dolphins had consumed two to five different species of cephalopods, while most stranded animals had consumed no or just one cephalopod species (usually *Loligo v. reynaudii,* a common epipelagic squid that could potentially be captured with relatively low energy expenditure). However, fewer stranded than non-stranded dolphins were examined, which could have affected these observations.

An additional concern for cetacean health is the bioaccumulation of pollutants. Results from Froescheis, Looser, Cailliet, Jarman, & Ballschmiter (2000) and Unger, Harvey, Vadas, & Vecchione (2008) showed that anthropogenic pollutants were being found in the tissues of deep-sea cephalopods, and were then bioaccumulating in their predators. Several cranchiid squid were listed in Unger et al. (2008), including *Teuthowenia megalops*, making this a potential health risk for any predator of *Teuthowenia* (see Table 3.1). It is increasingly evident that anthropogenic pollutants have far-reaching impacts in the ocean, even in remote habitats, and not just in coastal regions. Hoving et al. (2006) discussed pollutants in the water affecting the endocrine systems of marine life, causing intersexuality in a variety of organisms. Since anthropogenic pollutants are only recently being investigated, it is unknown what other effects these chemicals are having on marine organisms. Mammals like whales are interacting enough with the deep-sea ecosystem for this bioaccumulation to have potential negative health impacts, but more importantly, it should be emphasised that anthropogenic pollutants are making their way from coastal sources to the deep sea in the first place. Taxa like *Teuthowenia*, that have already been shown to carry

anthropogenic pollutants, can continue to be used in future research to monitor the health of deep-sea ecosystem.

Conclusion:

This meta-analysis shows that members of the genus *Teuthowenia* are eaten by more than a dozen species of predators across a variety of marine habitats ranging from the deep sea to coastal systems, and spanning most oceans. Although not a large part of most diets, even *T. pellucida,* which was previously thought to not be an important source of food, does appear trophically linked to several animals living in the southern hemisphere. Further efforts to understand *Teuthowenia's* trophic role more fully should focus on the diets of these squid, using stable isotope analysis augmented by molecular work where possible.

Conclusions

Cranchiid squids are abundant in most oceans (Laptikhovsky & Arkhipkin, 2003), yet little is known regarding their systematics, biology, or behaviours. This research has provided a more detailed description of one abundant species in New Zealand waters, *Teuthowenia pellucida*. Herein, the morphology of this squid has been described throughout ontogenetic development, trophic interactions of the genus have been analysed on a global scale, and the structure of the retina was examined to determine whether ontogenetic changes occur.

After examining *Teuthowenia pellucida* (~150 specimens), ranging in size from 1.5–210 mm dorsal mantle length, seven developmental stages were identified: three larval (Stages A–C), two juvenile (D, E), one sub-adult (F), and one adult. Morphologically distinguishing features of each stage were identified (see Table 1.1). As larval cranchiids can sometimes be difficult to identify accurately, characters have been identified to distinguish between larval *Teuthowenia*, *Megalocranchia* and *Liguriella*, which can appear similar.

Teuthowenia pellucida displays adult morphology at ~100 mm mantle length, and mature specimens have distinguishing modifications on their arms, which can be used for sexual identification and species differentiation. Beaks of *T. pellucida* showed phenotypic variation, with beaks of both sexes falling along a morphological spectrum between those illustrated in Figure 1.10. The other two species of *Teuthowenia* should also be examined for similar variability, which has implications for predator diet studies based on cephalopod beaks.

The *T. pellucida* material examined herein had been collected throughout New Zealand waters, covering a depth range of 0–1463 meters. Animals smaller than 50 mm ML were all collected in the photic zone, sub-adults of ~ 50–100 mm ML were mostly epipelagic, and most

larger specimens were found in deeper water. The ontogenetic descent observed in this species suggests trophic interactions with animals from both epipelagic and mesopelagic environments. In a meta-analysis of the trophic importance of the genus *Teuthowenia* (Table 2.1), both *T. pellucida* and *T. megalops* were found in the diets of several fish, seabird and cetacean species. *Teuthowenia maculata*, a species from the central Atlantic, was only documented in one study. The small amount of information on this species could be due to a lack of research done in this area. Therefore, to gain a more complete understanding of the trophic importance of this genus, more deep-sea cephalopod predation research should be conducted in the central Atlantic.

One of the most noticeable morphological characteristics of *Teuthowenia* are the proportionally large eyes of the adult, which are believed to maximise light perception in the aphotic environment. Retinal structure was examined in various developmental phases of *T. pellucida*; older specimens, on average, had longer photoreceptors, theoretically because longer photoreceptors would provide a greater ability to perceive low light levels in deeper water. Most specimens showed the previously documented linear photoreceptor structure; however, several also showed a "fanning" pattern that appears undescribed and requires further investigation. Cross-sections of the retina also showed a thin dark layer of a pigment called ommin. This pigment has previously been found to migrate from middle ommin layer of the photoreceptor to the outer receptor wall (Daw & Pearlman, 1974); material examined herein appears to confirm this. This migration created a screening layer of pigment that absorbs much of the incoming light and prevents over-stimulation of the photoreceptor. Visual capabilities of deep-sea squid have only recently been investigated, as modern technologies are allowing for deeper sampling, and this topic warrants further research.

Although the material examined in this research provides some additional knowledge in the field of cranchiid research, there is still much we do not know about this abundant family. Many of the genera in Cranchiidae have never been systematically reviewed, and several undescribed species are believed to exist. Given the abundance of the family in the deep sea, further research done on this family could have great trophic, physiological, and systematic importance to the state of knowledge of deep-sea cephalopods.

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Appendix 1: Material Examined

Stage	Specimens
Stage A (larval)	**30 specimens (all sex indet.):**
	NMNZ M.302130, ML 1.5 mm, NZ, RV *James Cook*, Stn J11/26/80, 1980
	NMNZ M.102180, ML 3.0 mm, 45˚28.2′S, 164˚50.9′E, NZ, 231 m over 4540m, RV *Kaiyo Maru*, Stn KM/231B/85, 29/08/1985
	NMNZ M.102209, ML 3.0 mm, 44˚45.3′S, 167˚1.1′E, NZ, 205 m over 2520 m, RV *Kaiyo Maru*, Stn KM/230A/85, 29/08/1985
	NMNZ M.302138, ML 3.0 mm, NZ, RV *James Cook*, Stn J13/08/81, 1981
	NMNZ M.286202, NZ, RV *James Cook*, Stn J11/54/81
	NMNZ M.302148, ML 3.4 mm, NZ, RV *James Cook*, Stn J10/**/80, 1980
	NMNZ N.102151, ML 3.6 mm, 45˚59.7′S, 165˚37.3′E, NZ, RV *Kaiyo Maru*, Stn KM/212C/85, 30/08/1985
	NMNZ M.302155, ML 4.0 mm, RV *James Cook*, Stn J11/11/81, 1981
	NMNZ M.302142, ML 4.0 mm, NZ, RV *James Cook*, Stn J10/**/80, 1980
	NMNZ M.102239, ML 5.0 mm, 46˚45.8′S, 165˚54.2′E, NZ, RV *Kaiyo Maru*, Stn KM/112B/85, 31/07/1985
	NMNZ M.302157, sex indet., ML 5.0 mm, RV *James Cook*, Stn J11/06/81, 1981
	NMNZ M.302135, ML 5.0 mm, NZ, RV *James Cook*, Stn J10/**/80, 1980
	NMNZ M.302149, ML 5.0 mm, NZ, RV *James Cook*, Stn J13/08/81, 1981
	NMNZ M.302147, ML 6.0 mm, NZ, RV *James Cook*, Stn J13/07/81, 1981
	NMNZ M.302144, ML 6.0 mm, NZ, RV *James Cook*, Stn J16/**/80, 1980
	NMNZ M.302150, ML 6.2 mm, NZ, RV *James Cook*, Stn J16/05/80, 1980
	NMNZ M.302146, ML 7.0 mm, NZ, Stn ACH/61/80, 1980
	NMNZ M.302156, ML 7.5 mm, NZ, RV *James Cook*, Stn J11/**/80, 1980
	NMNZ M.302129, ML 7.8 mm, NZ, RV *James Cook*, Stn J11/**/80, 1980
	NMNZ M.302130, ML 8.0 mm, NZ, RV *James Cook*, Stn J11/26/80, 1980
	NMNZ M.302145, ML 8.0 mm, NZ, RV *James Cook*, Stn J16/**/80, 1980
	NMNZ M.302131, ML 8.0 mm, NZ, RV *James Cook*, Stn J16/04/80, 1980
	NMNZ M.302143, ML 8.0 mm, NZ, RV *James Cook*, J11/**/80, 1980
	NMNZ M.302132, ML 8.0 mm, NZ, RV *James Cook*, Stn J11/26/80, 1980
	NMNZ M.302141, ML 8.2 mm, NZ, RV *James Cook*, J16/08/80, 1980
	NMNZ M.302133, ML 8.7 mm, NZ, RV *James Cook*, Stn J16/103/80, 1980
	NMNZ M.091592, ML 9.0 mm, 36˚46.8′S, 176˚18.5′E, NZ, 114m over 620m, RV *James Cook*, Stn J11/38/76, 31/07/1976
	NMNZ M.070961, ML 9.7 mm, 42˚56.5′S, 175˚7.0′E, NZ, 545 m, RV *Wesermunde*, Stn W05/133/79, 18/11/1979
	NMNZ M.302151, ML 10.0 mm, NZ, RV *James Cook*, Stn J09/16/83, 1983
Stage B (larval)	**4 specimens (all sex indet.):**
	NMNZ M.302139, ML 9.5 mm, NZ, RV *James Cook*, Stn J16/**/80, 1980
	NMNZ M.287201, ML 13.0 mm, NZ, RV *James Cook*, Stn J16/**/80, 1980
	NMNZ M.287203, ML 13.0 mm, NZ, RV *James Cook*, Stn J16/**/80, 1980
	NMNZ M.287202, ML 15.0 mm, NZ, RV *James Cook*, Stn J16/**/80, 1980
Stage C (larval)	**3 specimens (all sex indet.):**
	NMNZ M.286197, ML 19.0 mm, NZ, *HMAS Cook*, 06/1984
	NMNZ M.091551, ML 21.0 mm, 39˚14.9′S 178˚45.5′E, NZ, 30 m over 3000 m, RV *James Cook*, Stn J12/11/87, 14/09/1987

NMNZ M.287201, ML 27.0 mm, NZ, RV *James Cook*, Stn J16/**/80, 1980

Stage D (juvenile) **9 specimens (all sex indet.):**

NIWA 71677, ML 28.0 mm, 42.92˚S, 175.87˚E, NZ, 50 m, TAV002/20, Stn Z10384, 8/02/2001

NIWA 71678, ML 30.1 mm, 42.93˚S, 175.93˚E, NZ, 50 m, TAV002/19, Stn Z10383, 8/02/2001

NMNZ M.286142, ML 32.0 mm, 40˚55.6′S, 176˚50.3′E, NZ off Cape Turnagain, 30 m, RV *James Cook*, Stn J15/19/87, 09/12/1987

NMNZ M.287274, ML 33.4 mm, 42˚39.9′S, 174˚48.1′E, NZ, 30 m, RV *James Cook*, Stn J15/20/87, 9/12/1987

NMNZ M.286206, ML 34.0 mm, 40˚55.4′S, 176˚58.0′E, NZ, 30 m, RV *James Cook*, J15/18/87, 9/12/1987

NIWA 71679, ML 36.8 mm, 42.73˚S, 176.37˚E, NZ, 10 m, TAV002/33, Stn Z10397, 10/02/2001

NIWA 71681, ML 36.9 mm, 43.02˚S, 175.37˚E, NZ, 30 m, TAV002/1, Stn Z10365, 05/02/2001

NIWA 71680, ML 38.7 mm, 43.35˚S, 175.55˚E, NZ, 30 m, TAV002/16, Stn Z10380, 08/02/2001

NIWA 71713, ML 42.1 mm, Stn *TAN*0012/61, 01/12/2000

Stage E (juvenile) **15 Specimens (all sex indet.):**

NMNZ M.287275, ML 40.0 mm, 39˚16.3′S, 178˚34.6′E, NZ, 30 m, RV *James Cook*, Stn J15/05/87, 06/12/1987

NIWA 71718, ML 42.1 mm, 42.28˚S, 176.08˚E, NZ, 25 m, TAV002/87, Stn Z10525, 21/02/2001

NIWA 71676, ML 42.1 mm, 42.64˚S, 176.76˚E, NZ, 20 m, TAV002/18, Stn Z10456, 16/02/2001

NIWA 71714, ML 42.4 mm, 42.54˚S, 176.47˚E, NZ, 20 m, TAV002/35, Stn Z10473, 18/02/2001

NMNZ M.091421, ML 43.0 mm, 40˚8.3′S 160˚14.9′E, NZ, 45–35 m over 4700 m, RV *James Cook*, Stn J16/08/85, 16/10/1985

NIWA 71714, ML 46.3 mm, 42.54˚S, 176.47˚E, NZ, 20.0 m, TAV002/35, Stn Z10473, 18/02/2001

NIWA 71704, ML 49.6 mm, TAN802/213, 01/02/1998

NMNZ M.067849, ML 50.0 mm, 38˚22.15′S, 178˚57.18′E, NZ 30.0 m, RV *James Cook*, Stn J13/09/79, 30/09/1979

NMNZ M.091562, ML 50.0 mm, 39˚14.5′S, 179˚50.1′E, NZ, 30 m, over 3600 m, RV *James Cook*, Stn J12/17/87, 14/09/1987

NIWA 71715, ML 51.7 mm, NZ, 50 m, TAN9202/100, Stn Z8779, 24/02/1992

NMNZ M.067262, ML 52.0 mm, 37˚51.6′S, 179˚7.66′E, NZ, 30 m over 1700 m, RV *James Cook*, Stn J13/05/79, 30/09/1979

NMNZ M.286141, ML 60.0 mm, 41˚10.9′S, 176˚38.6′E, NZ, 1148–1170 m, RV *James Cook*, Stn J12/57/88, 24/10/1988

NMNZ M.091544, ML 62.0 mm, 39˚14.9′S, 178˚35.4′E, NZ, 30 m, RV *James Cook*, Stn J12/09/87, 13/09/87

NMNZ M.286199, ML 70.0 mm, 44˚38.3′S, 173˚40.2′E, NZ, 350 m over 887–924 m, RV *James Cook*, Stn J21/18/84, 10/12/1984

NMNZ M.286208, ML 73.0 mm, 39˚15.6′S, 179˚49.6′E, NZ, 30 m, RV *James Cook*, Stn J15/11/87, 07/12/1987

Stage F (sub-adult) **43 specimens (all sex indet.):**

NMNZ M.286140, ML 34.6 mm, 42˚36.6′S, 174˚36.4′E, NZ, 30 m, RV *James Cook*, Stn J15/21/87

NMNZ M.091544, ML 45.6 mm, 39˚14.9′S, 178˚35.4′E, NZ, 30 m, RV *James Cook*, Stn J12/09/87, 13/09/1987

NIWA 71706, ML 45.6 mm, TAN9802/179, 01/02/1998

NIWA 71693, ML 48.8 mm, 100–20 m, TAN9802/133, 01/02/1998

NMNZ M.067250, ML 50.0 mm, 37˚50.9′S, 179˚8.1′E, NZ, 40 m, RV *James Cook*, Stn J01/78/80, 11/01/1980

NMNZ M.074213, ML 50.0 mm, 42˚0.80′S, 174˚52.80′E, NZ, 1292–1395 m, RV *Tangaroa*, Stn 1979671, 14/01/1979

NIWA 71717, ML 52.0 mm, 42.55˚S, 174.75˚E, 80 m, TAV002/106, Stn Z10544, 22/02/2001

NMNZ M.074319, ML 52.0 mm, 37˚31.0′S, 178˚52.5′E, surface over 1080 m, RV *James Cook*, Stn J14/75/76, 20/11/1976

NIWA 71682, ML 54.0 mm, *NZI*, Stn u2308

NMNZ M.286151, ML 54.0 mm, 39˚26.44′S, 179˚51.83′E, NZ, 21–103 m over 2405 m, RV *Tangaroa*, Stn TAN9503/46, 28/03/1995

NMNZ M.091513, ML 54.0 mm, 32˚10.2′S, 167˚54.7′E, NZ, 60 m over 750–1125 m, RV *James Cook*, Stn J16/23/85, 24/10/1985

NMNZ M.091619, ML 54.0 mm, 38˚48.8′S, 172˚24.4′E, NZ, 120–180 m over 832–833 m, RV *Kaiyo Maru*, Stn KM/102B/85, 19/07/1985

NMNZ M.286163, ML 56.0 mm, 38˚58.87′S, 170˚7.38′W, NW of Valerie Guyot Louisville Ridge, 20–101 m over 4600 m, RV *Tangaroa*, TAN9503/14, 21/03/1995

NIWA 71708, ML 58.0 mm, TAN9802/189, 01/02/1998

NMNZ M.067845, ML 58.0 mm, 38˚22.05′S, 179˚35.35′E, NZ, 30 m over 1700 m, RV *James Cook*, Stn J13/11/79, 01/10/1979

NIWA 71699, ML 59.0 mm, TAN9802/211, Stn Z11021

NMNZ M.091599, 32˚15.3′S, 167˚45.6′E, NZ, 125 m over 1640–1678 m, RV *James Cook*, Stn J16/21/85, 24/10/1985

NMNZ M.286162, ML 61.0 mm, 40˚0.83′S, 177˚58.41′E, NZ, 14–99 m over 1529 m, RV *Tangaroa*, Stn TAN9503/35, 29/03/1995

NMNZ M.286188, ML 61.0 mm, 39˚14.76′S, 179˚18.36′W, NZ, 31–102 m over 3500 m, RV *Tangaroa*, TAN9503/1, 19/03/1995

NIWA 71687, ML 63.0 mm, 42.76˚S, 179.99˚W, 1064–750 m, TAN0104/43, 16/04/2001

NMNZ M.074361, ML 63.0 mm, 39˚9.5′S, 179˚22.5′E, NZ, 30 m over 1200 m, RV *James Cook*, Stn J08/45/80, 23/04/1980

NMNZ M.286139, ML 64.0 mm, 39˚45.40′S, 178˚34.46′E, NZ, 22–109 m over 2711 m, RV *Tangaroa*, Stn TAN9503/50, 28/03/1995

NMNZ M.286203, ML 65.0 mm, 40˚28.71′S, 170˚21.80′W, W of Valerie Guyot Louiswille Ridge, 16–104 m over 4300 m, RV *Tangaroa*, Stn TAN9503/35, 25/03/1995

NIWA 71702, ML 65.2 mm, 41.57˚S, 179.67˚E, 100 m, TAN9802/164, Stn Z10311

NMNZ M.074303, ML 67.0 mm, 37˚30.80′S, 177˚32.50′E, NZ, 715–755 m, RV *Tangaroa*, Stn 1979763, 24/01/1979

NMNZ M.286143, ML 67.0 mm, 43˚33.7′S, 167˚7.6′E, NZ, 170–250 m over 1250 m, RV *James Cook*, Stn J15/52/87, 16/12/1987

NMNZ M.074309, ML 68.0 mm, 37˚28.3′S, 177˚13.0′E, NZ, 80–386 m over

194–994 m, RV *James Cook*, Stn J07/56/75, 09/05/1975
NIWA 71717, ML 69.0 mm, 42.55˚S, 174.75˚E, 80 m, TAV002/106, Stn Z10544, 22/02/2001
NMNZ M.287271, ML 74.0 mm, 44˚41.59′S, 173˚18.92′E, NZ, 750 m over 890–987 m, RV *James Cook*, Stn J21/21/84, 11/12/1984
NIWA 71716, ML 76.0 mm, 42.44˚S, 174.74˚E, 100 m, TAV002/119, Stn Z10557, 23/02/2001
NMNZ M.286156, ML 76.0 mm, 40˚31.91′S, 178˚59.33′E, NZ 17–107 m over 3000m, RV *Tangaroa*, Stn TAN9503/59, 30/03/1995
NMNZ M.286144, ML 77.0 mm, 40˚30.64′S, 169˚53.89′W, W of Valerie Guyot Louisville Ridge, 17–103 m over 4350 m, RV *Tangaroa*, Stn TAN9503/33, 24/03/1995
NMNZ M. 074329, ML 78.0 mm, 37˚34′S, 177˚15′E, NZ, 420 m over 840 m, RV *James Cook*, Stn J07/50/75, 08/05/1975
NMNZ M.286152, ML 80.0 mm, 45˚11.3′S. 165˚20.7′E, NZ, 30 m, RV *James Cook*, Stn J15/46/87, 15/12/1987
NIWA 71707, sex indet., ML 81.0 mm, TAN9802/190, 01/02/1998
NMNZ M.012942, ML 84.0 mm, 41˚47′S, 175˚2′E, NZ, 732 m over 1463 m, 19.04.1957
NMNZ M.286189, ML 84.0 mm, 40˚17.61′S, 179˚36.19′E, NZ, 15–96 m over 3200 m, RV *Tangaroa*, Stn TAN9503/54, 29/03/1992
NMNZ M.091505, ML 87.0 mm, 32˚18.9′S, 167˚40.5′E, NZ, 150 m over 1451–1565 m, RV *James Cook*, Stn J16/20/85, 24/10/1985
NMNZ M.091411, ML 87.0 mm, 39˚42.1′S, 168˚0.1′E, NZ, 832–844 m, RV *James Cook*, Stn J05/46/84, 15/03/1984
NIWA 71700, ML 90.0 mm
NMNZ M.074306, ML 94.0 mm, 41˚39′S, 175˚14.48′E, NZ 140 m, RV *James Cook*, Stn J10/10/75, 28/06/1975
NMNZ M.074311, ML 94.0 mm, 30˚58.0′S, 175˚12.8′W, NZ, 971 m over 5000 m, RV *James Cook*, Stn J17/76/76, 15/12/1976
NMNZ M.286178, ML 96.0 mm, 39˚20.23′S, 179˚40.72′E, NZ, 20–105 m over 3958 m, RV *Tangaroa*, Stn TAN9503/45, 28/03/1995
NIWA 71673, ML range 62–117 mm, TAN 9802/212

Adult **30 specimens, (11 ♀, 13 ♂, 6 sex indet.):**
NMNZ M.283190, ♀, 41˚21.50′S, 176˚20.90′E, NZ, 1073–1116 m, RV *James Cook*, Stn J06/14/84, 03/04/84
NIWA 71686, sex indet., ML 100.0 mm, 700 m, Stn Z9917, 02/07/1997
NMNZ M.172982, ♂, ML 120.0 mm, 32˚32.25′S, 169˚43.56′E, Norfolk Ridge, 1275 m, RV *Tangaroa*, Stn 10, 12/05/2003
NIWA 71691, sex indet., ML 122.0 mm, SWA 9501/073, 26/07/1995
NIWA 71688, ♂, ML 135.0 mm, TAN9708/037
NMNZ M.286176, sex indet., ML 138.0 mm, 42˚50.2′S, 177˚32.3′W, NZ, 821–863 m, RV *James Cook*, Stn J12/42/84, 29/07/1984
NMNZ M.287267, ♂, ML 140.0 mm, 41˚10.9′S, 176˚38.6′E, NZ, 1148–1170 m, RV *James Cook*, Stn J12/57/88, 24/10/1998
NMNZ M.074307, ♂, ML 150.0 mm, 41˚50.4′S, 175˚44.0′E, NZ, 210 m over 2000 m, RV *James Cook*, Stn J10/03/75, 27/06/1975
NMNZ M.286159, ♂, ML 150.0 mm, 37˚39.8′S, 168˚58.4′E, NZ, 878–895 m, RV *James Cook*, Stn J04/41/83, 23/02/1983
NIWA 71672, ♀, ML 155.0 mm, 43.15˚S, 174.29˚W, 980–1021 m, Z8548,

07/08/1996
NIWA 71684, ♀, ML 155.0 mm, 44.00˚S, 178.00˚W, TAN9713/53, 13/12/1997
NMNZ M.144084, ♀, ML 156.0 mm, 42˚51.2′S, 175˚33.1′E, NZ, 695 m, Stn 1112/62, 02/07/1998
NIWA 71694, sex indet., ML 159.0 mm, 42.45˚S, 170.11˚E, 826 m, Stn Z9845, 05/09/1999
NMNZ M.102592, ♀, ML 160.0 mm, 40˚18.74′S, 173˚15.93′E, North of Tasman Bay, 75–78 m, RV *Cordella*, COR9001/035, 19/02/1990
NMNZ M.172926, ♂, ML 160 mm, 32˚32.25′S, 169˚43.56′E, Norfolk Ridge, 1275 m, RV *Tangaroa*, Stn 10, 12/05/2003
NMNZ M.067224, sex indet., ML 165.0 mm, 43˚6.77′S, 174˚15.97′E, NZ, 494–508 m, RV *James Cook*, Stn J07/05/79, 02/06/1979
NMNZ M.286186, ♂, ML 167.0 mm, 37˚32.9′S, 169˚25.9′E, West of Cape Egmont, 1075–1106 m, RV *Arrow*, Stn A04/174/83, 26/10/83
NIWA 71695, sex indet., ML 170.0 mm, 44.63˚S, 176.02˚W, 948–931 m, Stn Z8551
NMNZ M.091717, ♂, ML 170.0 mm, 39˚46′S, 178˚4′E, NZ, 1050–1089 m, FV *Wanaka*, Stn WK4/71/86, 20/04/1986
NMNZ M.286160, ♂, ML 173.0 mm, 40˚32.8′S, 168˚40.5′E, NZ, 937–942 m, RV *James Cook*, Stn J02/33/87, 09/02/1987
NIWA 71670, ♂, ML 178.0 mm, 42.81˚S, 176.73˚E, 1063–1069 m, Stn Z8311, 19/07/1995
NIWA 71675, ♀, ML 180.0 mm, 42.70˚S, 177.35˚E, 950 m, Stn Z9565, 02/12/1998
NMNZ M.286191, ♂, ML 184.0 mm, 41˚18.3′S, 176˚23.9′E, Wairarapa coast, 1175–1191 m, RV *James Cook*, Stn J9/7/89, 12/09/1989
NIWA 71674, ♀, ML 185.0 mm, Stn Z11124
NIWA 71691, ♂, ML 185.0 mm, SWA 9501/073, 26/07/1995
NMNZ M.283190, ♀, ML 185.0 mm, 41˚21.50′S, 176˚20.90′E, NZ, 1073–1116 m, RV *James Cook*, Stn J06/14/84, 03/04/1984
NIWA 71690, ♀, ML 190.0 mm, RV *Tangaroa*, TAN 9708/13
NIWA 71671, ♀, ML 200.0 mm, 42.92˚S, 179.41˚E, 759 m, Stn Z8501, 19/06/1996
NMNZ M.117199, ♀, ML 201.0 mm, 42˚44.26′S, 176˚34.27′W, 1196–1203 m, RV *Tangaroa*, Stn TAN9206/207, 14/07/1992
NMNZ 287265, ♂, ML 210.0 mm, 42˚28.4′S, 169˚31.9′E, NZ, 1016–1020 m, RV *James Cook*, Stn J04/12/83, 17/02/1983