Gut contents of a giant squid *Architeuthis dux* (Cephalopoda: Oegopsida) from New Zealand waters

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Abstract New diet information for the giant squid (*Architeuthis dux*) is presented based on the identification of substantial identifiable prey items recovered from the gut contents of a specimen caught in New Zealand waters. Prey items are attributed to two species of squid: *Nototodarus* sp. and *Architeuthis dux*. The incidence of *Nototodarus* in the stomach contents is not new, but the occurrence of *Architeuthis* remains is. Numerous fragments of an *Architeuthis* tentacular club, consisting of carpus, manus, and dactylus suckers, and the dactylic pouch, introduce the possibility of cannibalism—a hitherto unreported behaviour in this genus. A synopsis of *Architeuthis* diet is presented and alternatives to cannibalism (such as autophagy) are evaluated.

Keywords cannibalism; *Architeuthis*; *Nototodarus*; Mollusca; Cephalopoda; diet

INTRODUCTION

No stomach caecum found amongst the more than 100 giant squid specimens (*Architeuthis dux*) previously examined by the authors has contained more than trace fish bone, scale, and unidentifiable squid remains. However, a recent routine dissection of one specimen revealed a stomach caecum distended with food items. The present caecum is significant in three ways: the contents include many identifiable hard-part remains; the inventory of known prey items is increased; and, once identified, the prey composition proves quite remarkable, without precedent in giant squid.

Popular and scientific interest in *Architeuthis* has been sparked by its reputed rarity and superlative size. An increased incidence of capture in recent years has also produced increasingly regular reports of distribution, morphology, and data available post-mortem (such as diet).

The diet of *Architeuthis* has previously been described (e.g., Toll & Hess 1981; Forch 1998; Lordan et al. 1998; Ré et al. 1998) only from identification of trace recognisable prey-item remains from gut contents. Moreover, because of the fragmentary nature of remains, attribution of prey items to genus or species is usually provisional at best.

The most detailed reports of *Architeuthis* diet are those of Forch (1998) and Lordan et al. (1998). Förch reports 8 species of fish (7 of which were rattails (Macrouridae) and 1 tentatively identified as orange roughy (*Hoplostethus atlanticus*)), 2 types of crustacean (chelae of 1 unidentified species, and 5 identified species of copepod), and 2 species of squid (*Moroteuthis ingens* and *Nototodarus sloanii*), in the diet of New Zealand *Architeuthis*. Lordan et al. (1998) report fish (*Trachurus trachurus* and *Micromesistius poutassou*), crustaceans (*Nephrops norvegicus*), bivalves (*Modiolus phaseolinus*), cephalopods (*Todarodes sagittatus*, *Eledone cirrhosa* (from statoliths) and tentatively *Taonius pavo*), several ascidians, unidentified cestode and nematode species, and small stones in the diet of *Architeuthis* from Irish waters.

Toll & Hess (1981) report gut contents containing unidentifiable cephalopod and fish remains; Roper & Young (1972) similarly describe the gut of one juvenile as containing much unidentifiable amorphic material and a few small fish bones. Pérez-Gándaras & Guerra report beaks of squids *Histiotethys* sp. and *Ommastrephes caroli* (1978), and much-masticated, unidentifiable cephalopod remains from adult specimens (1989). Similarly
unidentifiable cephalopod remains (nine large squid suckers of 13–16 mm diameter, lacking sucker rings) are reported from an adult by Zeidler & Gowlett-Holmes (1996).

The more unusual items that have been reported from the stomachs of *Architeuthis* include pebbles (Ré et al. 1998), the alga *Fucus* sp. (Kjennerud 1958), unidentified algae (Nordgård 1928; Aldrich 1991), and cestodes (Pippy & Aldrich 1969).

This dietary synopsis shows that deep-water pelagic cephalopods and fish are prevalent in gut contents of trawled *Architeuthis*, and that a surprising diversity of shallow-water benthic or sessile organisms may also appear in the guts of stranded specimens. Whether adult *Architeuthis* is a benthopelagic or truly pelagic species remains unconfirmed.

**MATERIALS AND METHODS**

The gut contents reported here were recovered from the stomach caecum of an extensively damaged (mantle only, of 1.6 m length) mature female *Architeuthis*. No capture data accompanied the carcass. Although unlocalised, this specimen is known to have been caught in New Zealand waters by hoki trawl, and was probably taken between 400 and 600 m depth off one of two locations: either West Coast South Island, near to Hokitika Canyon, during July and August, or Banks Peninsula, East Coast South Island, between December and February.

Dissection revealed a caecum distended with prey. The caecum was cut open, the frozen contents photographed *in situ*, removed, defrosted in a bucket and then fixed in 5% carbonate-buffered formalin solution for 24 h. Fixed contents were then passed over a 1-mm sieve, rinsed in fresh water, and transferred to 40% carbonate-buffered isopropyl alcohol for preservation. Alcohol-preserved samples were subsequently passed over a 1-mm sieve, the contents placed into trays and manually screened, and identifiable prey remains extracted and sorted for subsequent identification.

By process of elimination, prey items were identified through comparison with a complete reference collection of New Zealand squid species. The caecal contents were critically compared with equivalent structures from locally occurring squid species. Stomach contents have been accessioned into the biological collections of the Auckland University of Technology (AUT), Earth & Oceanic Sciences (EOS) Research Institute, accession # AUT G.22.

Collection acronyms used in text are: AUT, Auckland University of Technology; NMNZ, Museum of New Zealand; and NZOI, the National Institute of Water & Atmospheric Research Ltd (NIWA), formerly the New Zealand Oceanographic Institute.

**RESULTS**

In addition to much unidentified cephalopod soft tissue, the caecum contents (Fig. 1) comprised: the posterior portion of a squid mantle, with gladius; several separate gladius fragments; an intact buccal bulb, with beaks, oesophagus and intestine; an anterior portion of mantle with paired inverted-T-shaped mantle-locking cartilages; one T-shaped funnel-locking cartilage; one nearly intact arm of length 107 mm, bearing many suckers with strong distal- to disto-lateral dentition (8 long teeth) and smooth proximal margins, and numerous shorter arm fragments possessing suckers with comparable dentition. All of these remains are attributed to a species of *Nototodarus*. Two cephalopod eyes and 4 small, disassociated cephalopod eye lenses cannot reliably be attributed to any taxon due to lack of systematic characters, although they are probably also referable to *Nototodarus*. The largest of these prey remains (a near-intact portion of mantle, with paired mantle-locking cartilages) was of 69 mm length, 33 mm relaxed diameter and 19 mm compressed dimension (preserved measures).

Both smooth and dentate sucker rings were represented amongst the gut contents. Smooth sucker rings vary from ~2 to 4.5 mm diameter, while dentate sucker rings, divisible into two groups, are <1 mm in diameter (with 7–9 teeth distributed around the distal- and disto-lateral margins) and 5–13.5 mm diameter (with 18–25 uniform small-sized teeth evenly distributed around the margin).

The larger suckers are of a type and size consistent with those found on the tentacle club of *Architeuthis dux*, and as they cannot be differentiated from voucher samples, we conclude that they are from the same species.

The caecal contents also included portions of a tentacle club dactylus, with dactylitic pocket and 10 intact, smooth-ringed suckers (Fig 5–7), in addition to 23 unlocalised detached suckers with smooth sucker rings, 3 with attached knobs. The latter are attributable to either carpal or dactylic portions of a tentacle club. Numerous tentacular sucker-ring fragments (greatest fragment depth 8 mm) (Fig. 2, 3), and 62 suckers with intact sucker rings, each with
18–25 sharp-pointed, similarly sized projecting teeth, with sucker and sucker ring greatest diameters 14.0 and 13.5 mm, respectively (Fig. 4) were also present.

**DISCUSSION**

**Morphology of sucker rings**

Several unrelated genera of squid have sucker rings superficially similar to those described here. To support the above attribution of smooth and larger dente-urate sucker rings to *Architeuthis*, we here briefly discuss sucker ring dentition in these other groups.

Post-paralarval onychoteuthid squid (Onycho- teuthidae) have smooth sucker rings. Three genera are known from New Zealand waters (*Notonykia*, *Onychoteuthis*, and *Moroteuthis*). The diameter of the largest smooth sucker rings recovered from the *Architeuthis* gut contents (4.5 mm) exceeds that of locally occurring mature specimen of any *Notonykia* or *Onychoteuthis* species (1.8 mm [Female (F), mantle length (ML) 177 mm, NMNZ M.160475] and 1.9 mm [F, ML 137 mm, NMNZ M.74145], respectively). The smooth sucker ring of *Moroteuthis* can be differentiated from that of *Architeuthis* by its eccentric ring aperture surrounded by a raised, narrow ridge, and a pronounced basal notch (Fig. 8–10).

The two cranchiid genera *Teuthowenia* and *Galiteuthis* have sucker-ring dentition varying from smooth to dente- te (Voss 1980, 1985). The sucker rings of New Zealand specimens of these genera conform to those illustrated in Voss (locs cit.), although some rings possess more developed dentition than earlier reported (Fig. 11, 12). The eccentric ring aperture of these taxa similarly serves to differentiate them from those of *Architeuthis*.

The largest arm suckers on both *Nototodarus sloanii* and *N. gouldi* possess 7–9 pointed teeth distributed around the distal and disto-lateral margins (Dunning & Förch 1998), and voucher samples are inseparable from the smaller suckers found in the *Architeuthis* gut contents.
The larger fragmented sucker rings bear only a superficial resemblance to those of Todarodes filippovae and T. angolensis, in that they are of large size. The tentacle club medial manus sucker rings of these two species are characterised by 7–13 and 13–16 long-pointed teeth respectively (Dunning & Wormuth 1998), while the equivalent suckers on the related Ommastrephes bartrammi have a single greatly enlarged tooth in each sucker ring quadrant (Dunning 1998). The largest intact sucker rings attributed to Architeuthis, recovered from the Architeuthis gut contents, have the 18–25 similarly sized teeth characterising this genus (Förch 1998).

The diet of Architeuthis

Although prey items must be well masticated by cephalopods in order to pass through the narrow oesophagus (maximum relaxed diameter 10 mm in this specimen), one prey fragment recovered from the stomach caecum was of 69 mm greatest dimension, and 19 mm compressed dimension; many other fragments were of comparable size. It appears that Architeuthis dispatches prey by slicing it into large pieces and passing them down the oesophagus. Nevertheless, the dimensions of larger prey items are at striking odds to the diameter of the relaxed oesophagus, especially given that the oesophagus in cephalopods passes directly through the brain.

As algae are reported only from the gut contents of stranded specimens (Aldrich 1991, specimen # 10; Nordgård 1928; Kjennerud 1958), we do not believe them to be a natural component of Architeuthis diet. Rather we suggest that a drying or struggling squid might gnash its beak against algal-covered rocks before stranding. Stones, reported from the stomachs of both stranded and trawled specimens (Lordan et al. 1998; Ré et al. 1998), must also be an unnatural component in Architeuthis diet, and are likely to have been secondarily ingested with prey items in in-situ captured specimens, or ingested in a similar way to algae in stranded specimens. The bivalve (Modiolus phaseolinus), small ascidians, and unidentified cestode and nematode species described from the stomach caecum of Architeuthis (Lordan et al. 1998) are both therein and here considered to be secondarily ingested. The copepods reported from stomach caecal contents in three of Förch’s specimens (numbers 2, 4, and 12) may also have been secondarily ingested, although, given the regularity of occurrence it is also possible that they actually parasitise the caecum.

Pelagic fish and cephalopod remains prevailed in the gut contents of trawl-caught specimens (Pérez-Gándaras & Guerra 1978, Toll & Hess 1981, Förch 1998, and the present report), and squid were also present in the caecum of the floating specimen reported by Zeidler & Gowlett-Holmes (1996). We believe that pelagic squid and fish are the natural diet of Architeuthis dux, and that it appears that it is a pelagic species, rather than a benthic-pelagic one.

Most Architeuthis caught by trawl in New Zealand waters have been associated with the hoki fishery, trawled from between 400 and 600 m. To the best of our knowledge, only one Architeuthis specimen has ever been caught during deeper-water (>800 m) trawling for orange roughy (Förch 1998), and none of the 105 specimens received over the past 7 years, examined by the present authors, was taken by orange roughy trawl. Surprisingly, then, a report of orange roughy within gut contents of an Architeuthis exists, although the identification was tentative only (Förch 1998). Also unusual, given the close association between the hoki fishery and the incidence of Architeuthis capture in the water column, is the absence of hoki in the diet of Architeuthis. Instead, other macrourid fish and squid dominate in the diet of regionally captured specimens. Thus, it appears that Architeuthis probably preys on the same food items as hoki (small fish, prawns and squid), instead of on the hoki itself.

Accidental self-ingestion, autophagy or cannibalism

Because dactylic suckers, marginal and fragmented manus suckers, and carpal suckers with knobs still attached were recovered from the stomach contents of this Architeuthis, we conclude that portions of an entire tentacle club have been consumed, perhaps as an aftermath of inter-architeuthid aggression or mating. It is possible that the large unidentified suckers reported by Zeidler & Gowlett-Holmes (1996) from an Architeuthis stomach caecum are referable to

Fig. 2–4  Architeuthis tentacle club manus sucker rings: 2, 3 medial sucker ring fragments; 4, marginal sucker ring, lateral profile; scale bar 10 mm. 5–7 Architeuthis tentacle-club carpal-sucker rings: 5, oral; 6, aboral; and 7, lateral perspectives; scale bar 5 mm. 8–10 Moroteuthis ingens arm sucker rings (NMNZ M.12952): 8, oral; 9, aboral; and 10, lateral perspectives; scale bar 3 mm. 11, 12: Cranchiid mid-arm sucker rings: 11, Teuthowenia pellucida (NMNZ M.160610); 12, Galiteuthis sp. (NZOI Stn Z8791); scale bar 1 mm.
Architeuthis, which would then constitute another record of either cannibalism or autophagy in the genus.

Regeneration of a damaged tentacle club has been reported for Architeuthis (Aldrich & Aldrich 1968), so the loss of the club has precedent and need not be fatal. Aldrich later describes (1991, p. 474) a beached specimen (# 15) as unique amongst those he had encountered, in that it clearly showed evidence of having engaged in battle with what was apparently another cephalopod. He bases this conclusion on evidence of sucker scars ranging from 2.7 to 4 mm in diameter on some arms, in addition to the ends of incomplete arms being serrated in a manner unlike that associated with beaching. Aldrich (1991, p. 475) attributes this damage to combat with another architeuthid. Our report of large tentacular sucker rings of Architeuthis from a stomach caecum, and that of Zeidler & Gowlett-Holmes (1996), of large unidentifiable suckers recovered from a conspecific stomach, equally support Aldrich’s contention that damage through combat with other architeuthids is possible. Whether intentional or not, ingestion of an entire Architeuthis tentacle club does constitute cannibalism.

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