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# Unleashing the Kraken: on the maximum length in giant squid (*Architeuthis* sp.)

C. G. M. Paxton

Centre for Research into Ecological and Environmental Modelling University of St Andrews, St Andrews, UK

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*Architeuthis*; *Physeter*; gigantism; anecdotal reports; giant squid; maximum size; body size estimates.

**Correspondence**
Charles G. M. Paxton, Centre for Research into Ecological and Environmental Modelling University of St Andrews, The Observatory, Buchanan Gardens, St Andrews, Fife KY16 9LZ, UK.
Email: cgp2@st-andrews.ac.uk

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## Abstract

Giant squid are among the largest invertebrates known, but a consensus on their maximum size is lacking. Statistical investigation of various measures of body length and beak size in *Architeuthis* suggests that squid of at least 2.69 m (99.9% prediction interval: 1.60–3.83 m) mantle length (ML) may be handled by large bull sperm whales but perhaps not females. Given the relationship of squid ML to standard (from tip of mantle to end of arms) and total (from tip of mantle to end of tentacles) length, the observed spread of individual lengths, along with a longest reliably measured ML of 2.79 m, purported squid of 10 m standard length and even 20 m total length are eminently plausible.

## Introduction

Giant squid (Mollusca, Cephalopoda, Architeuthidae, *Architeuthis dux* Steenstrup, 1857) are one of the most enigmatic large marine animals on the planet. Strandings of specimens recognisable as this species in Europe date back to 1639 (see Ellis, 1999, for a history), probably not (Paxton & Holland, 2005) 1545/1546, as often stated. It was described (*in*formally) only in 1855–1860 (Steenstrup, 1857; Ellis, 1999) and photographed alive in its natural environment only in 2004 (Kubodera & Mori, 2005). Ever since its discovery, there has been considerable speculation as to its maximum size (Heuvelmans, 1968; Aldrich, 1991; Ellis, 1999; Roper & Shea, 2013) and since only *c.* 460 specimens (pers. obs.) of giant squid have ever been in some sense measured compared to *c.* 700 reported as of 2015 (summed from Guerra *et al.*, 2011; Roper *et al.*, 2015 and other sources), it is obvious that the probability that the longest individual is among those catalogued is extremely low.

There are several methods that could allow elucidation of maximum lengths of giant squid: (a) anecdotal reports, (b) estimation of an asymptotic length from growth curves, (c) estimation of length from sucker scars on whales, (d) measurement of available specimens, and (e) extrapolation of total length (TL) based on recovered beaks knowing the relationship of beak size to body length.

Anecdotal reports (see Table 1) of estimated great lengths in what are presumably specimens of *Architeuthis* are generally far longer than any measured specimens. As reports of animals of great size are often subject of inaccuracies and exaggerations (e.g. Murphy & Henderson, 1997), it remains moot whether these reports are accurate.

Methods (b) and (c) are not considered in detail because of uncertainties in the growth rate of giant squid (Grist & Jackson, 2007) and uncertainties associated with the maximum observed scar diameter which may grow with the animals and whether the said scars can be attributed to *Architeuthis*.

Direct measurement is obviously the most robust way to estimate sizes, but material is often fragmentary and not all measurements are taken. In addition, TL (i.e. the length of the entire animal from the tip of the mantle to the ends of the tentacles, 'entire length' is also used for this measurement) of even intact animals is subject to noise because of post-mortem elasticity of the two long tentacles (Verrill, 1879) and changes due to preservation (Förch, 1998). Standard length (SL, the length of the animal from the posterior end of the mantle to the furthest end of the intact eight arms, 'whole length' is sometimes also used for this measurement) provides a more robust estimate of length as does measurement of the mantle length (ML) alone. It is this latter length that is most commonly recorded.

Also of interest is the maximum length of a squid that could be taken by a sperm whale *Physeter macrocephalus*. O'Shea & Bolstad (2008) suggested that sperm whales could eat the largest squid, but offered no formal quantitative argument.

**Table 1** Recorded and estimated *Architeuthis* extreme lengths

| | ML (m) (dorsal ML except where unspecified) | SL (m) (i.e. mantle + head + arms) | TL (m) (i.e. mantle + head + tentacles) |
|---|---|---|---|
| Longest measured | 3.35 (Dell, 1952; Förch, 1998) SP[a]<br>More reliably 2.79, (Kirk, 1880) SP | 9.45 (Verrill, 1879) NA | Measured? 19 (Berzin, 1972) I<br>16.81 (Kirk, 1888) SP<br>16.76[b] (Verrill, 1879) NA |
| Longest visually estimated | *c.* 30.48 (T. Lipington pers. comm.) NA<br>4 (Lynch, 2014) I | *c.* 53.34 (Starkey, 1963) I<br>*c.* 30.48 (Braun) NA | *c.* 18.29 (Murray, 1874) |
| Longest remains reported associated with sperm whale feeding | Measured:<br>2.4? (Keil, 1963)[c] NA<br>1.98 (Clarke, 1955, 1956)[d]NA | Visually estimated: *c.* 9 (Hansford, 2009)[e] NP<br>Definitely measured: 4.96 (Clarke, 1956) NA | Measured?: 19 (Berzin, 1972) I<br>Definitely measured: 10.49 (Clarke, 1956) NA |

All measurements in m.

N.B., not all specimens have all dimensions measured; ML, mantle length; SL, standard length; TL, Total length. Abbreviations indicate region: NA, North Atlantic; SA, South Atlantic; I, Indian ocean; NP, North Pacific; SP, South Pacific.

[a]A 4.5 m specimen from Mauritius is often mistakenly cited but consultation of the primary paper (Staub, 1993) reveals an ill-defined length which is clearly not ML.

[b]Sometimes mistakenly cited as 17.37 m (57 ft) but the source is clear that it is 55 ft long.

[c]From a 16 m male sperm whale in the Azores in August 1961. However, the account is confused and the 2.4 m figure probably refers to the head and ML combined.

[d]From a 14.3 m male sperm whale landed in the Azores in 1955.

[e]Not clear how much/what portion of body was eaten.

Using the relationship of squid beak size (typically measured as lower rostral length) to ML provides a method to estimate the length of the squid eaten by sperm whales where the beaks frequently persist in the gut of the whale (Clarke, 1980, 1986). However, it should be noted that beaks also can be possibly subject to post-mortem shrinkage upon drying or storage in alcohol (Verrill, 1879) and to a much lesser extent if at all, eroded in the gut (i.e. in seals; Grellier & Hammond, 2006).

Thus, the aim of these analyses was to explore body length of *Architeuthis* using a variety of different data, as well as updating previous analyses (Roeleveld, 2000) of the relationships between ML and beak size with the aim of determining the maximum size of squid taken from a sperm whale and plausible estimates of standard and TLs from the largest ML known.

## Materials and methods

Data were collected from a variety of reliable sources to compile a database of the above measurements. A major initial source was Sweeney & Roper (2001), but primary scientific references (e.g. Nesis *et al.*, 1985; Compagno Roeleveld & Lipinski, 1991; Cherel, 2003; Wada *et al.*, 2015) were sourced in almost all cases. Note that citations used for specimens are not given in the reference list for brevity. Only measured (as opposed to visually estimated) reported lengths of the squid dimensions were used, so many accounts could not be considered. Four measurements of length were of interest: ML ($n$ = 164), SL ($n$ = 39 with a ML measurement), TL ($n$ = 47 with a ML measurement) and rostral length of the lower beak ($n$ = 46 specimens with a ML measurement). ML was of most interest as this had the largest sample size and presumably ML is less likely to be subject to post-mortem changes compared to SL or TL. Also of interest were more anecdotal accounts of the maximum length of giant squid for comparison with the measured lengths. In keeping with recent research (Winkelmann *et al.*, 2013), I assumed *Architeuthis* is one species but see Discussion. Four statistical analyses were undertaken:

1 The effect on reported ML of sex (male, female or unknown) and mode of discovery (captured in nets, stranded, found floating, found in sperm whales or found in a predator that is not a sperm whale) was considered in a generalized linear model (GLM), assuming a Gaussian error structure with a log link. A $P < 0.01$ inclusion principle was implemented based on type II sums of squares. Model selection was backward.

2 ML was regressed against beak size (measured as lower rostral length), thus allowing a prediction to be made from the largest beak so far found in a sperm whale. The additional variables of sex and mode of discovery were also considered. The data were fitted as a GLM with a gamma error structure with a log link. Model selection was as above. Unlike Roeleveld (2000), I regressed ML on beak size rather than the other way around.

3 SL was regressed against ML (with additional variables of sex and mode of discovery albeit without the three-way interaction because of a paucity of combinations). The data were fitted as a GLM with a gamma error structure with an identity link. Model selection was as above. Only specimens with at least one intact arm were considered.

4 TL was regressed against ML (with additional variables of sex and mode of discovery). Only specimens with at least one intact tentacle were considered. The data were fitted as a GLM with a gamma error structure with an identity link. Model selection was as above. To make the analysis conservative, an exceptional specimen with very long intact tentacles discovered from Lyall Bay, North Island, New Zealand in 1887 was omitted (see Discussion).

For all regressions, *prediction* intervals as well as confidence intervals were estimated as *the range of sizes of individuals*, rather than the uncertainty in the mean response was of primary interest. A 99.9% criterion was used to visualise the potential spread in the population. Prediction interval estimation was by simulation from the parameters and covariance matrix of the original model. All statistical work was undertaken in the R statistical package (R Developmental Core Team 2014, v.3.1.3).

## Results

Table 1 provides a summary of various *maximum* claims of mantle, standard and TLs of giant squid from the literature. Of interest is that anecdotal accounts of squid length are considerably greater than measured accounts suggesting possible bias.

In the first analysis, 25% of the deviance in ML could be explained with sex and mode of capture (Fig. 1). The model met standard diagnostics. MLs of squids found in sperm whales were smaller than in squids found by other means apart from in predators that were not sperm whales. The well-established sexual dimorphism of this species is also shown.

The GLM of ML on beak size (measured as lower rostral length) and sex (Gaussian error, log link) suggested that only beak size was a predictor of ML (Fig. 2). The addition of the three disjunct juveniles from Wada *et al.* (2015), far smaller than and distinct from any previous published measured specimens, made model fitting to the larger animals difficult. Hence, these three animals were not included in this analysis. The fitted model met standard diagnostics except a large negative residual associated with the largest rostral length. This influential point was retained as it made the model more conservative (see below).

To the best of my knowledge the largest known swallowed beak (0.022 m lower rostral length) was from a male sperm whale caught at Madeira in 1959 (Clarke, 1962, 1986). The second largest beak (0.020 m lower rostral length) was from a male (12.50 m) caught at Durban in February 1964 (Clarke, 1980). The former gave a prediction of 2.69 m ML (99.9% prediction interval: 1.60–3.83 m, Fig. 2), considerably longer than the longest measured mantle (Table 1) actually found in remains associated with sperm whales. The prediction interval on this estimate also encompasses the longest mantle ever measured independent of sperm whales (Table 1). The extrapolation is conservative in that the highest *x*-value in the regression, the 0.0205 m beak (from an *immature* 1.8 m ML female (Gonzalez *et al.*, 2002) decreases the upward trend in the graph.

No effect of mode of capture was found on the relationship of SL to ML. There was a sex main effect, but this was simply that individuals of unidentified sex were unsurprisingly smaller than identified males and females. Thus, the model was re-fitted without sex. The final model met standard diagnostics. The best-fit line and intervals are given in Fig. 3.

In the case of the regression of TL on ML, no other variables were found to contribute to the variation and the fitted model met standard diagnostics. The smallest recorded specimen had high leverage. The specimen from Lyall Bay, New Zealand (see above), which was not used to fit the model,

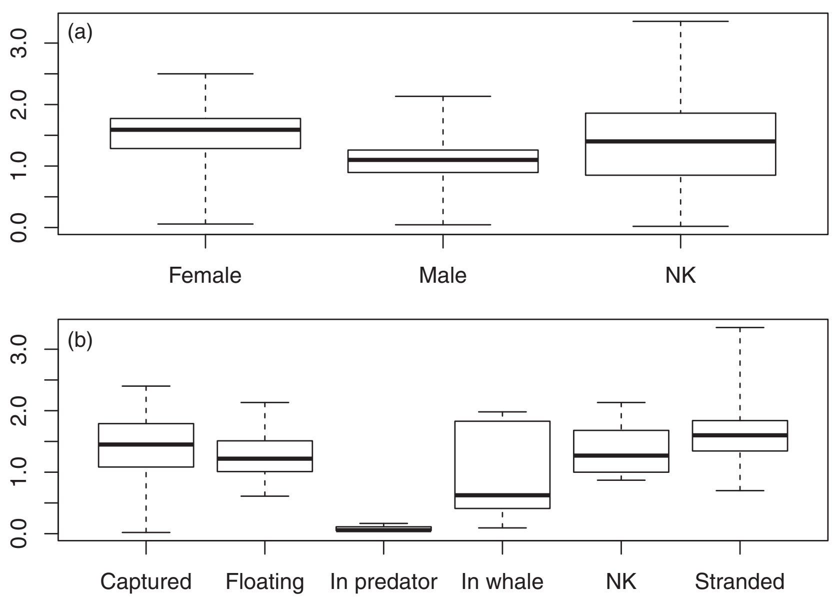


**Figure 1** Boxplots (minima, lower quartile, median, upper quartile, maxima), of mantle length in *Architeuthis* (m) (a) by sex and (b) by mode of capture. NK, not known.

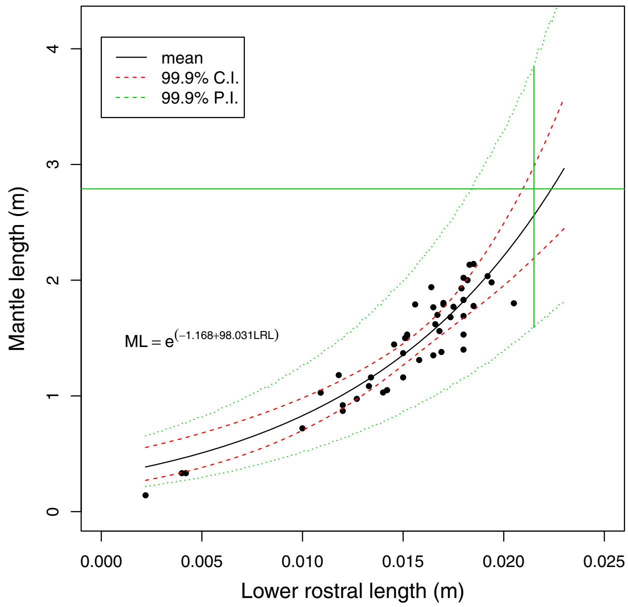


**Figure 2** Relationship of beak size (lower rostral length) to mantle length (ML) in *Architeuthis*. Mean, best-fit line; C.I., confidence interval; P.I., prediction interval. The vertical green line indicates the 99.9% prediction intervals for the largest beak found in a sperm whale. The total explained deviance was 77%. The horizontal green line shows the longest reliably measured ML of 2.79 m. N.B. The three shortest specimens were not considered in the fit. Intervals are extrapolated to these specimens for interest.

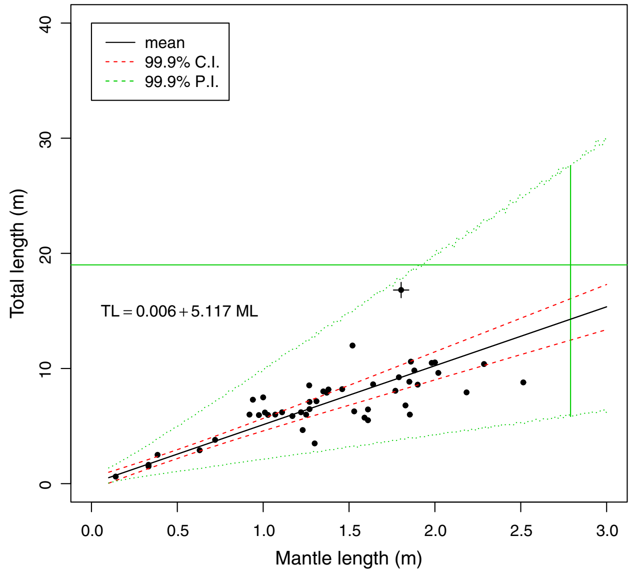


**Figure 4** Relationship of total length to mantle length (ML) in *Architeuthis*. Mean, best-fit line; C.I., confidence interval; P.I., prediction interval. The total explained deviance was 77%. The horizontal green line indicates Berzin's 19 m TL claim from the Indian Ocean. The cross indicates values taken from the exceptional specimen with long tentacles found stranded in Lyall Bay, North Island, New Zealand, in 1887. The 99.9% prediction interval for the longest ML measured reliably (2.79 m) is given by the vertical green line.

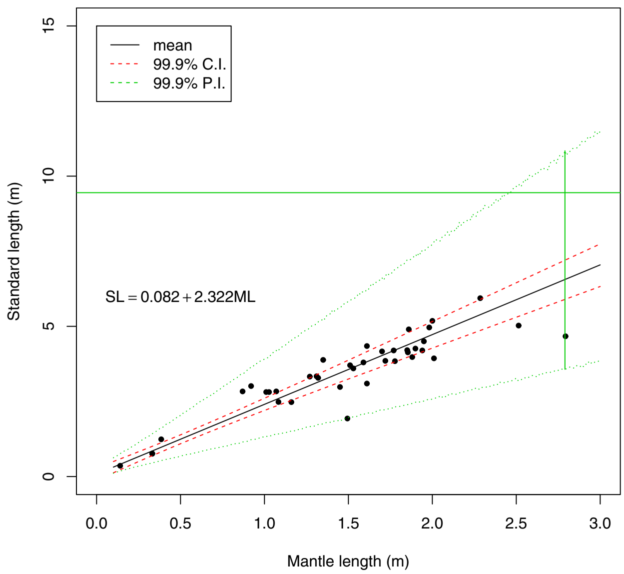


**Figure 3** Relationship of standard length (SL) to mantle length (ML) in *Architeuthis*. Mean, best-fit line; C.I., confidence interval; P.I., prediction interval. The total explained deviance was 88%. The horizontal green line indicates the longest SL yet measured 9.45 m. The 99.9% prediction interval for the longest ML reliably measured (2.79 m) is given by the vertical green line.

stands out, as it is just at the edge of the 99.9% prediction interval (Fig. 4).

# Discussion

Clarke (1980) argued on the basis of pigmentation of the beaks that the majority of *Architeuthis* taken by sperm whales were immature, but clearly large whales can take large squid and there are anecdotal reports of large squid material with whales (Table 1). Ignoring the 19 m TL claim (footnote to Table 1), the beak data here suggest *Architeuthis* of ML of up to *c.* 3 m could be taken by sperm whales. Based on the 99.9% prediction intervals, it does not seem implausible that even giant squid of the maximum ML so far measured (Table 1) could be eaten by sperm whales, although squid from whales were shorter on average than those stranded, found floating or captured in fishing gear (Fig. 1). However, there may be a bias here, as smaller *Architeuthis* specimens found unassociated with sperm whales may not be recognised and reported. As the largest beaks and/or MLs were found in sperm whales greater than 11 m long, the approximate maximum length of females (Whitehead, 2003), it is possible that the largest *Architeuthis* may outgrow predation by female sperm whales. More data are needed to clarify the maximum size of squid ingested by whales. That female squid grow larger than males may imply that female fecundity has been a selection pressure for large size but it is plausible that predation pressure, especially from female sperm whales at lower latitudes could also play a role.

*Architeuthis* do not occur at high latitudes (Roper, Sweeney & Nauen, 1984) where male sperm whales spend much of their lives (Whitehead, 2003).

Anecdotally, lengths of *c.* 30 (Braun, 1999) and *c.* 53 m (Starkey, 1963) have been claimed for animals seen near or at the surface and as squid do not generally leave their tentacles exposed except when grabbing prey and this appears to be the case for *Architeuthis* (Schwerin, 2013), presumably these reports would represent SLs. T. Lipington (pers. comm.) reported a ML of at least 30 m. Further, there is the more modest claim of Packard (1873) that 'old fishermen' claim that squid exceed the size of sperm whales in 'northern seas' that is presumably the largest bull sperm whales *c.* 18 m (Whitehead, 2003). Certainly there is good evidence that adult lengths vary considerably in *Architeuthis*, so SLs on the latter scale would seem improbable, but not wholly impossible given the observed lengths. However, given that giant squid can reach a ML of 2.79 m (Table 1), the estimated prediction intervals and that the longest measured SL is 9.45 m, squid up to 10 m, at the very least, SL would seem very probable indeed.

The accuracy of the two longest measured TLs of 19 and 16.81 m from a specimen found in the gut of a sperm whale from the Indian Ocean and from the specimen from New Zealand in 1887, respectively, should also be questioned but again are certainly not impossible. The New Zealand specimen (named *Architeuthis longimanus* Kirk, 1888) clearly has the largest ratio of TL to ML ever known in *Architeuthis* (Fig. 4) which led Bolstad & O'Shea (2004) to suggest that the length was paced out and/or there was extensive post-mortem stretching. However, a re-reading of the original paper suggests that the specimen, although initially paced out, was actually measured, nevertheless the TL is at the edge of the 99.9% prediction interval range (Fig. 4) and so it was certainly an unusual specimen. Berzin's (1972) Indian Ocean claim is suspect because of the roundness of the figure, the lack of detailed measurements and because in an associated photo, the mantle (whose length was not given) does not look very large compared to the men in the image. Consequently the measurement, if accurate, would represent another animal with very long tentacles. Winkelmann *et al.*'s (2013) molecular analysis of giant squid from around the world did not include either of these two specimens, so it remains possible that *Architeuthis longimanus* is a discrete species/subspecies from all other *Architeuthis dux*.

It is possible that much of the width of the prediction interval, in the case of the TL on ML regression, is due to a lack of large specimens and, of course, there is a small amount of extrapolation. Nevertheless, given that giant squid can reach MLs of 2.79 m (Table 1) and the estimated prediction intervals, squid with a conservative TL of 20 m would seem likely based on current data. This is with no correction for elasticity except for the omission of the suspect 1887 specimen. It would be useful to determine the limits of such elasticity in *Architeuthis* to constrain these estimates and determine if the 1887 specimen really was stretched. However, if elasticity was a general consequence of stranding, for example, this ought to be detectable in the data and this does not appear to be the case and there is at least one claim of post-mortem shrinkage of tentacles (Murray, 1874).

Length in *Architeuthis* was briefly discussed by McClain *et al.* (2015) where they seem to suggest that the distribution of lengths in *Architeuthis* should be normal. It is unclear why this should be so given the sexual dimorphism and sample they analysed was presumably a mix of ages. They also provided a regression of TL on ML (based on log transformed lengths) but did not provide a confidence or prediction interval. They had more data than considered here, but from their account they presumably used data from specimens with incomplete tentacles.

There was no evidence from these analyses that sex influenced the ratio of arms and tentacles. Males may be smaller than females (Fig. 1) but they are not differently proportioned.

O'Shea & Bolstad (2008) stated that of the 130 *Architeuthis* specimens they encountered, none exceeded 2.25 m ML and 13 m TL, but assuming a population of hundreds of thousands (from Roper & Shea, 2013), there are plenty of opportunities for animals to reach longer lengths and the *conservative* statistics strongly suggest this. I would argue that *Architeuthis* slightly larger than those proposed by O'Shea and Bolstad are probable and such a claim is not such a 'disservice to science' as they suggest.

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## Data accessibility

The datasets supporting this article have been uploaded as part of the Supporting Information.

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## Conflict of interests

I have no competing interests.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Code S1.** Code for squid analysis.
**Data S1.** Data for squid analysis.