Sexual dimorphism in the beaks of Moroteuthis ingens Smith, 1881 (Cephalopoda: Oegopsida: Onychoteuthidae)

K. S. BOLSTAD
Earth & Oceanic Sciences Research Institute
Auckland University of Technology
Private Bag 92006
Auckland 1020, New Zealand
kbolstad@aut.ac.nz

Abstract Sexual dimorphism in size and morphology of the lower beak of the warty onychoteuthid squid Moroteuthis ingens is analysed. Beaks of maturing males exhibit a band of weak, clear cartilage across the shoulder region, while mature males exhibit a pronounced excavation of this area; the hood remains intact. Female beaks attain greater size, but relatively shorter lower rostral lengths (LRL) than those of males; they display neither the shoulder cartilage nor later erosion, but the hood is consistently eroded in mature specimens. The angle ridge in females is considerably longer than in males. Due to the difference in LRL relative to overall beak size, M. ingens beaks from predator stomachs should be sexed prior to calculating prey size using LRL; for both sexes, the LRL-mantle length (ML) relationship is linear while the LRL-weight relationship is exponential. Sex-specific equations are provided for reconstructing ML and weight using LRL. Based on several incidences of male-female pairs collected with beaks interlocked, M. ingens is postulated to mate in a head-to-head position, with both individuals incurring beak damage during the event.

Keywords Dimorphism; mating; behaviour; biomass estimation; cephalopod beaks; Moroteuthis ingens; Onychoteuthidae

INTRODUCTION
Beaks of the warty onychoteuthid squid Moroteuthis ingens Smith, 1881 occur frequently and in large numbers in the stomach contents of sperm whales and other predators in New Zealand waters (Gaskin and Cawthorn 1967a,b; Clarke & Roper 1998; pers. obs.), indicating that this species comprises a major portion of the local prey. However, M. ingens remained largely unstudied and poorly understood for most of the past century. Several recent studies have partially remedied its obscurity, by reporting its diet (Jackson et al. 1998; Phillips et al. 2001, 2003a,b; Cherel & Duhamel 2003), and some aspects of its reproduction (Jackson & Mladenov 1994, Jackson 2001) and distribution (Jackson 1993; Jackson et al. 2000). Nesis (1995) hypothesises that M. ingens (which is unhectocotylised, like all other reported onychoteuthid taxa) may mate head-to-head, but its mating behaviour remains otherwise unknown.

Sexual dimorphism in adult size has been previously reported in M. ingens (Jackson et al. 1997), but no dimorphism in morphological characters is currently known for it or any other onychoteuthid. Dimorphism has, however, been reported in the beaks of the related Pholidoteuthis massyae (O’Shea et al. unpubl.), and is of particular significance, since it complicates identification of cephalopod taxa in the stomachs of teuthophagous predators. Where unrecognised, beak dimorphism may also compromise the accurate estimation of prey biomass, since historical formulae for calculating mantle length (ML) and weight from lower rostral length (LRL) are specific to genus or species, but not sex or maturity.

The following beak descriptions and equations (describing the relationship between submature to adult LRL, wet preserved weight, and ML) will aid the subsequent recognition and correct identification of the dimorphic beaks of male and female M. ingens, and help produce more accurate calculations of the size and weight of the squid prey taken by cetaceans. The new formulae are used to calculate the biomass of prey represented by a large number of M. ingens beaks from the stomach of a sperm whale.
MATERIALS AND METHODS
Material was examined from two repositories in Wellington, New Zealand: the Museum of New Zealand Te Papa Tongarewa (NMNZ), and the National Institute for Water and Atmospheric Research Ltd (NIWA, formerly NZOI). Beaks of 66 (formalin-fixed, 70% EtOH preserved) specimens of *M. ingens* were examined to ensure accurate records of species, sex and size; LRLs were measured using digital calipers. More than 500 preserved beaks collected from the stomach contents of a sperm whale stranded locally in the 1990s (New Zealand, unlocalised) were also examined. Morphological terminology for lower beaks, and cuts for shoulder and lateral-wall cross-sections, follow Clarke (1980). Mantle length (ML) was measured dorsally. MINITAB 14 software was used to calculate regression lines and the standard errors of the coefficients (Appendix 1).

**MATERIAL EXAMINED:** (*Moroteuthis ingens*):
Female (2 specimens): NZOI Z9427, maturing (unmated), ML 430 mm, 44°18.77′S, 178°13.35′W; NMNZ M.74296, spent (mated), ML 300 mm, 46°32′S, 166°09′E, 597–625 m, 24/11/1976, FV *Shinkai Maru*.
Mixed sex (60 specimens from NMNZ and NZOI collections): 34 female *M. ingens*, ML 76–487 mm, 26 male specimens, ML 76–365 mm, 42°46.98–53°13.84′S, 169°55.83′E–174°17.49′W.
Stomach contents (ex *Physeter macrocephalus*): NMNZ (unaccessioned), 140 male *M. ingens* lower beaks and 3 male *M. ingens* buccal bulbs, LRL 8.68–9.75 mm; 386 female *M. ingens* lower beaks and 7 female *M. ingens* buccal bulbs, LRL 9.13–12.85 mm.
In the sperm whale stomach contents examined, nearly all soft tissue had been digested away, leaving only the beaks. Ten semi-digested buccal bulbs remained, including one pair of intact buccal bulbs locked together by mutual biting.

RESULTS

Systematics
Female beaks attain larger overall size and greater absolute LRLs than those of males (maximum observed female LRL 12.85 mm; male c. 10.3 mm); by approximately ML 150 mm, the male LRL is longer relative to beak height and width, and to ML, than that of the female (Fig. 1, 2).

Submature male lower beaks are characterised by a large insertion of clear cartilage at the shoulder (Fig. 3–5), which forms a broad band across the wing from the rostrum to the wing’s posterior margin, interrupting the otherwise normal pigmentation. The jaw angle, rostrum, and corresponding wing regions of the submature female beak are comprised of uniformly smooth, dark chitin, and lack any transparent cartilage in the region of the jaw angle (Fig. 6–8A). At maturity, the beak of the female is overall darker and more robust, with thickened lateral walls and lateral wall fold. In females that have mated (evidenced by spermatophores implanted in the mantle...
Fig. 6–8A Lower beaks of submature female *Moroteuthis ingens*, NZOI Z9427, mantle length 430 mm, lower rostral length 9.5 mm. (6), Entire lower beak, lateral view; (7), entire lower beak, oblique view; (8), entire lower beak, oblique view. Scale bar (A) = 10 mm.

Fig. 8B–I, 9, 10 Lower beaks of mature female *Moroteuthis ingens*, NMNZ M.74296, mantle length 350 mm, lower rostral length 11.2 mm. (8B), Entire lower beak, oblique view; (C), anterior section through right lateral wall; (D), posterior section through lateral wall; (E–I), sections through: (E), lower wing; (F), middle of wing; (G), upper wing, below jaw angle; (H), jaw angle; (I), rostrum above jaw angle. Scale bars (8B), (9), (10) = 10 mm. Arrows indicate hood erosion.
musculature or viscera), the apex of the lower beak hood is consistently eroded or chipped away (Fig. 8B–10). Conversely, the hood remains intact in males, while the lower beak rostrum is excavated or eroded, having lost the transparent cartilage (Fig. 11–13). Beaks with this lower rostral excavation, when observed in situ in the buccal bulb, may be “dislocated”, i.e., the usual position of the beaks (upper rostrum within lower) is reversed (Fig. 14). The wings of the lower beak surround the upper beak as normal, but the rostral tip of the lower beak is positioned within the rostrum of the upper beak, opposite to the “natural” position. Beaks of maturing males, with non-excavated rostra, have not been observed in this dislocated position; however, the beaks of one female buccal bulb from the stomach contents of a sperm whale were also reversed in this fashion.

Fig. 11–13  Lower beaks of mature male Moroteuthis ingens, NZOI TAN0219/138, mantle length 270 mm, lower rostral length c. 10 mm. (11), Entire lower beak, lateral view; (12), entire lower beak, oblique view; (13A–H) as in (5A–H) through left lateral wall. Scale bars: (11), (12), (13A) = 10 mm. Arrows indicate jaw excavation.

Fig. 14  Buccal bulb of mature male Moroteuthis ingens, NMNZ M.131972, mantle length 362 mm, with upper beak inverted from its natural position or “dislocated”. Scale bar = 10 mm.
The lower beaks of all adult *M. ingens* share the following character states. Viewed in lateral profile, beak length and depth are subequal—some beaks are deeper than long, and some longer than deep (Table 1), but in many beaks, the longer measure is not immediately apparent. The hood length is approximately 30% of the baseline, apart from mature females. The crest is curved in the anterior 30–50% of its length, thereafter straightening and sloping “downward” in a steep line that parallels the basal/inner margin of the lateral wall. The posterior hood margin (where intact) lies close to the crest. The hood and wings are broad (where intact) and cover half the lateral wall; the wing width is approximately equal to the length of jaw edge. The jaw angle is obtuse (approximately 100°), and (where intact) is barely obscured by a broad, low, rounded wing fold. The crest is broad, and thickened to varying degrees (Fig. 5B,C; 8C,D; 13B,C; Table 1). There is no distinct shoulder ridge. The jaw forms a sharp cutting edge, widening rapidly into a rounded hood (Fig. 5H, 8I, 13H). The lateral wing fold parallels the slope of the crest for the anterior 50% of its length, thereafter sloping sharply downward, terminating at the approximate midpoint of the posterior lateral wall margin. Healing beak tissue (surrounding breaks/tears) forms initially as

**Fig. 15, 16** Swelling of the lower mandibular muscle of male *M. ingens*. (15), Left lateral view of intact swelling (indicated by arrow); (16), right lateral view of cross-section through swelling. Scale bars = 10 mm.

**Fig. 17** Interlocked buccal bulbs of male and female *Moroteuthis ingens* from the stomach of a sperm whale stranded in New Zealand. **A**, Left view of both buccal bulbs; **B**, right view. Scale bars: (A) = 10 mm; (B) = 8 mm.
Table 1  Sexually dimorphic character states in lower beaks of submature and mature/spent Moroteuthis ingens. Terminology follows Clarke (1962, 1980, 1986).

<table>
<thead>
<tr>
<th>Beak character</th>
<th>Submature female</th>
<th>Mature female</th>
<th>Submature male</th>
<th>Mature male</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length versus depth in lateral profile</td>
<td>Deeper than long</td>
<td>Length and depth approx. equal</td>
<td>Longer than deep</td>
<td>Longer than deep</td>
</tr>
<tr>
<td>Pigmentation</td>
<td>Nearly black anteriorly, fading rapidly to brown/amber on wing margins</td>
<td>Nearly black, fading to dark brown only at wing margins</td>
<td>Nearly black anteriorly, fading rapidly to pale amber on wing margins</td>
<td>Nearly black, fading to dark brown only at wing margins</td>
</tr>
<tr>
<td>Cartilage</td>
<td>Narrow anterior wing insertion</td>
<td>None</td>
<td>Broad band across wing from jaw angle, wide anterior inset into wing</td>
<td>Narrow anterior wing insertion; thin veneer covers broken/excavated chitin surfaces</td>
</tr>
<tr>
<td>Length of jaw edge (% wing length)</td>
<td>50% wing length</td>
<td>40% wing length</td>
<td>80–90% wing length</td>
<td>80–90% wing length</td>
</tr>
<tr>
<td>Shape of jaw edge</td>
<td>Slightly curved along entire length</td>
<td>Proximal 80% straight, distal 20% curved</td>
<td>Proximal 60% straight, distal 40% curved</td>
<td>Proximal 60% straight, distal 40% curved</td>
</tr>
<tr>
<td>Hood length (% of baseline)</td>
<td>30% baseline</td>
<td>Greatly eroded; remaining portion c. 10% baseline</td>
<td>30% baseline</td>
<td>40% baseline</td>
</tr>
<tr>
<td>Visible crest length (% of baseline)</td>
<td>30% baseline</td>
<td>50% baseline</td>
<td>50% baseline</td>
<td>40% baseline</td>
</tr>
<tr>
<td>Wing width</td>
<td>Uniform along wing length</td>
<td>Uniform along wing length</td>
<td>Narrowest at jaw angle, widening distally</td>
<td>Narrowest at jaw angle, widening distally</td>
</tr>
<tr>
<td>Crest thickening</td>
<td>Pronounced</td>
<td>Pronounced</td>
<td>Very slight</td>
<td>Very slight</td>
</tr>
<tr>
<td>Lateral wall indented below crest</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Lateral wall fold</td>
<td>Semi-circular in cross-section; somewhat thickened</td>
<td>Semi-circular in anterior cross-section; thickened into ridge</td>
<td>Broad, low, only slightly thickened</td>
<td>Broad, low, only slightly thickened</td>
</tr>
</tbody>
</table>

soft transparent cartilage, presumably hardening and darkening into chitin over time (Fig. 11–13).

While most lower beaks of *M. ingens* may be immediately identified based on the shape of the hood and rostral regions (and especially any observed excavation/erosion of the same), several less obvious features also vary according to sex and maturity (Table 1) and may be useful in identifying beak fragments.

In several males with rostral erosion, a pronounced swelling of the lower mandibular muscle was observed, forming a hard, spherical knot of tissue some 10–15 mm in diameter directly below the lower hood (Fig. 15, 16). The swollen tissue is uniformly muscular; no alien object or variation in structure was observed in cross-section. This phenomenon has not been observed in any females or submature males.
Large numbers of both lower beak types (140 males, 131 with rostral excavation, LRL 8.68–9.75 mm; 386 females, all with hood erosion, LRL 9.13–12.85 mm) were present in the stomach of a sperm whale stranded in New Zealand. Ten buccal bulbs, also present in the stomach contents, retain the lower or both beaks, and include one pair of intact buccal bulbs locked together by mutual biting (Fig. 17A,B). These beaks are inverted in orientation, with each lower rostrum biting the other, and each upper rostrum biting the hood region of the opposing beak, positioning one squid “upside down” relative to the other.

The stomach caeca of all mature male and all mature and spent female specimens examined were shrunken and empty. A number of parasitic nematodes (Anisakis sp.) were found in the caecum walls and surrounding membranes of many specimens of ML 145 mm and greater.

**Biomass estimation**

The LRL-ML and LRL-weight relationships are sex-specific (Fig. 1, 2) and have been presented together for the purpose of comparison between males and females.

The relationship between LRL and dorsal mantle length (ML) is linear for both sexes (Fig. 1):

For females, \((ML) = 40.44(LRL) – 14.7\)

\(r^2 = 0.94, n = 32\)

LRL coefficient 40.44, standard error 1.92

Constant coefficient –14.72, standard error 21.05

For males, \((ML) = 32.023(LRL) + 8.31\)

\(r^2 = 0.91, n = 26\)

LRL coefficient 32.023, standard error 2.03

Constant coefficient 8.31, standard error 12.46

The relationship between LRL and weight is exponential for both sexes (Fig. 2):

For females, weight = 1.9976(LRL^{2.8899})

\(r^2 = 0.96, n = 31\)

LRL coefficient 2.8899, standard error 0.1062

Constant coefficient 1.9976, standard error 0.392

For males, weight = 3.3332(LRL^{2.4067})

\(r^2 = 0.94, n = 24\)

LRL coefficient 2.4067, standard error 0.1323

Constant coefficient 3.3332, standard error 0.715

The weight of females with LRL >6 mm (ML >250 mm) was somewhat variable due to differing states of maturity. The greatest weight is attained at the height of maturity, prior to spawning, due to development of nidamental glands and eggs.

**DISCUSSION**

In addition to the new morphological information reported herein, this study supports and links the conclusions reached by several prior studies examining aspects of *M. ingens* beaks and their relationship to body size and weight. Lipinks & Linkowski (1986) recognised that the relationship between ML and weight for this species was sex-specific; Jackson (1995) concluded the same for the LRL-weight relationship. Reliable beak differentiation on the basis of morphology, starting from a relatively small size (LRL c. 4.5 mm), may henceforth enable investigators to consider new information such as the sex ratio of *M. ingens* taken as prey. This information may enable more accurate estimates of squid biomass from beak samples.

**Estimating squid biomass**

Beak dimorphism and erosion may ultimately prove a common trait within this group (rendering revisions in beak identification keys and size/weight calculations necessary). For comparison, the theoretical combined weight of the 60 reference specimens measured for this study (measured in actuality as 28.6 kg) was calculated using several historical LRL-weight formulae given for *M. ingens*. The formula given by Clarke (1986) for all Moroteuthis species yields an estimate of 59.8 kg for the present specimens; the logarithmic formulae given by Jackson (1995) estimate 48 kg; and the sex-specific LRL-weight formulae herein yield an estimate of 29.8 kg. The difference between the formulae may reflect fixation-related changes in size and weight (see Andriguetto & Haimovici 1988). It is therefore recommended that such formulae, when given or revised for other taxa in the future, should be as specific as possible (certainly to species and, where applicable, sex), and should detail the fixation and treatment history of the specimens examined, to ensure accurate estimations of prey biomass.

**Mating behaviour of *M. ingens***

The presence of more than 500 beaks almost exclusively attributable to *M. ingens* in the stomach of one sperm whale suggests an aggregation of conspecifics; further evidence points, more specifically, to a spawning aggregation. All beaks in the stomach
were of a size consistent with near-mature to spent M. ingens (male LRLs 8.68–9.75, female LRLs 9.13–12.85 mm), and nearly all beaks possessed those character states (excavation of the rostrum in males and erosion of the hood in females) associated with mature to spent individuals. Moreover, two buccal bulbs from this sample, one male and one female, were locked together in a mutual bite. Head-to-head mating in M. ingens has been postulated by Nesis (1995), and Jackson & Jackson (2004) report the capture of a male-female pair of M. ingens that were locked together, beak to beak. The damage observed in both male and female beaks at maturity could be reasonably explained by beak-to-beak mating (the cartilaginous insert seen in submature male beaks would be damaged, or completely excavated, by prolonged grinding against the hardened lower rostrum of the female). Nearly all individuals represented in this stomach content sample would therefore have mated.

In combination, these observations suggest the following: that the foraging sperm whale found a spawning or post-spawning aggregation of M. ingens, and consumed many individuals and at least one mating pair; and that M. ingens, in its spawning aggregations, mates in a head-to-head posture, facilitating the implantation of spermatophores into the anterior margin of the female’s mantle, by insertion of the very large and presumably quite manoeuvrable penis (one mature male observed was 250 mm ML, with a penis length of 330 mm, Fig. 18).

The inverted orientation of the locked buccal bulbs (Fig. 17A,B), and the primarily dorsal and dorso-lateral implantation of spermatophores reported by Jackson & Jackson (2004), also suggest that one mating individual may commonly be positioned “upside down” relative to the other (i.e., the female’s Arms I positioned against the male’s Arms IV and vice-versa). The hood damage observed in mature females is consistent with the position of the male’s upper rostral tip during an inverted bite, while the female’s longer upper rostrum passes over the male’s lower hood, leaving it intact. The “dislocation” observed frequently in mature male beaks (and infrequently in females), with the upper rostrum positioned outside the lower, may result from the extended gape required to accommodate the other’s beak during mating, preventing the beaks from returning to their natural position as the bite is released. Similar hood erosion to that observed in mature/spent female M. ingens has been observed in one spent female specimen of M. robsoni Adam, 1962 (pers. obs.), suggesting that it may follow a similar mating strategy.

ACKNOWLEDGMENTS

Many thanks to I. Anderson, University of Auckland, for his photographic assistance, F. Gomez for insightful discussions, access to materials, and ongoing interest, D. Corbett, P. Rebstock and N. Binnie for statistical advice, and to M. Norman and N. Molschaniwskyj for constructive comments on this manuscript. Thanks also to S. O’Shea, Auckland University of Technology, to B. Marshall, Museum of New Zealand Te Papa Tongarewa, and to G. Jackson, University of Tasmania. This research was supported by the Auckland University of Technology and the American Museum of Natural History.
REFERENCES


Appendix 1 – Statistical analysis of regressions

Regression Analysis: Female ML versus Female LRL
The regression equation is: \( ML = -14.7 + 40.4(LRL) \)
32 cases used, 3 cases contain missing values

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coef</th>
<th>SE Coef</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-14.72</td>
<td>13.99</td>
<td>-1.05</td>
<td>0.301</td>
</tr>
<tr>
<td>LRL</td>
<td>40.441</td>
<td>1.921</td>
<td>21.05</td>
<td>0.000</td>
</tr>
</tbody>
</table>

\( S = 31.3952 \) R-Sq = 93.7% R-Sq(adj) = 93.4%

Regression Analysis: Male ML versus Male LRL
The regression equation is: \( ML = 8.3 + 32.0(LRL) \)
26 cases used, 4 cases contain missing values

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coef</th>
<th>SE Coef</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>8.31</td>
<td>12.46</td>
<td>0.67</td>
<td>0.511</td>
</tr>
<tr>
<td>LRL</td>
<td>32.023</td>
<td>2.026</td>
<td>15.81</td>
<td>0.000</td>
</tr>
</tbody>
</table>

\( S = 28.4157 \) R-Sq = 91.2% R-Sq(adj) = 90.9%

Regression Analysis: Female Weight versus Female LRL
The regression equation is: \( \text{weight} = 1.9976(LRL^{2.8899}) \)
31 cases used, 4 cases contain missing values

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coef</th>
<th>SE Coef</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>1.9976</td>
<td>c. 0.392*</td>
<td>3.54</td>
<td>0.001</td>
</tr>
<tr>
<td>ln LRL</td>
<td>2.8899</td>
<td>0.1062</td>
<td>27.21</td>
<td>0.000</td>
</tr>
</tbody>
</table>

\( S = 0.276616 \) R-Sq = 96.2% R-Sq(adj) = 96.1%

*95% confidence interval for 1.9976 is (1.340, 2.978)

Regression Analysis: Male Weight versus Male LRL
The regression equation is: \( \text{weight} = 3.3332(LRL^{2.4067}) \)
24 cases used, 6 cases contain missing values

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coef</th>
<th>SE Coef</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>3.3332</td>
<td>c. 0.7147**</td>
<td>5.66</td>
<td>0.000</td>
</tr>
<tr>
<td>ln LRL</td>
<td>2.4067</td>
<td>0.1323</td>
<td>18.20</td>
<td>0.000</td>
</tr>
</tbody>
</table>

\( S = 0.358611 \) R-Sq = 93.8% R-Sq(adj) = 93.5%

**95% confidence interval for 3.3332 is (2.144, 5.182)