1 # Dwarf males of giant warty squid *Kondakovia*
2 # *longimana* and a description of their
3 # spermatophores

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14 **Abstract**

15   Antarctic squid are widely known to play an important role in the diet of various Antarctic
16 predators, although the biology of those squid and how that relates to their availability to their
17 predators is poorly known. We assessed the reproductive system of the deep-sea giant
18 warty Antarctic squid *Kondakovia longimana* under a predator-prey context. The spermatophores of
19 male *K. longimana* are described, based on two specimens foraged by albatrosses at Bird Island,
20 South Georgia (54°S, 38°W). Spermatophore length (SL) was 42–90 mm, head occupied mean = 1.8–
21 2.4% SL, ejaculatory tube = 17–22% SL, cement body = 19–22% SL, seminal reservoir = 56–59% SL
22 and rear empty part = 0.4–0.8% SL. All spermatophores of *K. longimana* in our study were normal
23 and functional, and very dissimilar to those of other spent squid, in which the spermatophores have
24 short, semi-transparent seminal reservoirs and a large empty rear part. Senescent male *K.
25 longimana* could become available to predation by albatrosses (presumably being surfaced) with
26 spermatophoric sacs (Needham's sacs) containing at least a hundred of normal spermatophores
27 having no evidence of reproductive system degeneration. From known relation between beak and
28 body size all known adult males in *K. longimana* were dwarfs in respect to females. Our data also
29 show that they have extended spermatophore production as in other squids.

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Introduction

34   Antarctic squid is a major component in the diet of numerous predators of the Southern

35   Ocean all through the year, ranging from small penguins to large toothed whales (Xavier and Cherel

36   2009). Little is known about reproduction of the Antarctic squid (Nesis et al. 1998; Laptikhovsky and

37   Arkhipkin 2003; Collins and Rodhouse 2006). Indeed, there is still considerable debate to how

38   Antarctic squid (particularly those living and feeding in deep waters) become available to

39   surface/near-surface feeders, such as albatrosses (Xavier et al. 2013). One of them, the giant warty

40   squid, *Kondakovia longimana* Filippova, 1972, inhabits Antarctic epi- and mesopelagic waters and

41   also occurs near the sea floor (Nesis 1987; Collins and Rodhouse 2006). Adult *K. longimana* are an

42   important prey species for sperm whales *Physeter macrocephalus* and elephant seals *Mirounga*

43   *leonina*, whereas sub-adults and juveniles are preyed upon by albatrosses and penguins (Cherel and

44   Weimerskirch 1999; Xavier and Cherel 2009). Little is known about reproduction of *K. longimana*

45   species, but its life span may take several years and it might be a polycyclic spawner (Bizikov 1991;

46   Jarre et al. 1991; Laptikhovsky et al. 2013). Females of *K. longimana* of < 670 mm mantle length (ML)

47   and up to 7 kg body weight (BW) have been reported as immature, with gonad weights of about 1–

48   2% BW (Clarke 1980; Bizikov 1991). A few, large females of this species, which were found

49   occasionally at the surface, and one captured by a longline, were 670–1080 mm ML (7–30 kg BW)

50   (Clark 1980; Vacchi et al. 1994; Lu and Williams 1994; Lynnes and Rodhouse 2002; Laptikhovsky et al.

51   2013). There has only been one report of a mature male (Clarke 1980), which was 350 mm ML and

52   ca. 1 kg BW and was found in a sperm whale stomach.

53   The original description of the species was based on three small immature females (Filippova

54   1972). A schematic drawing of the spermatophore of *K. longimana* was provided by Clarke (1980),

55   who stated that this one mature male specimen known to science had spermatophores in two

56   narrow-sized groups: 51.3–55.5 mm and 81.5–82.6 mm (23.3-23.6% ML). Until now, no further

57   mature male specimens have been reported (Bolstad 2008).

58   Spermatophores and other parts of soft bodies are known to be found in stomach contents

59   and boluses of adult albatrosses (Cherel and Weimerskirch 1999; Xavier et al. 2003 a,b; Xavier et al.

60   2004), that together with fresh beaks, allow identification of these body parts (Clarke 1962; Clarke

61   1980; Xavier et al. 2005). This also provides an opportunity for a taxonomically important description

62   of the spermatophores of *K. longimana,* as the earlier description of a single spermatophore (Clarke

63   1980) did not provide key information and has been viewed as "difficult to interpret" (Hess 1987).

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66   **Materials and methods**

67   Reproductive systems of two male *K. longimana* (identified by fresh beaks attached directly

68   to body tissues) were found in the food of two albatross species at Bird Island, South Georgia (54

69   °01S, 38°03W) in September 2009:

70   Sample A - stomach contents of a chick of Wandering Albatross *Diomedea exulans* L. were

71   collected following Xavier et al. (2003a). After a parent fed its chick, the chick was inverted over a

72   bucket and its stomach contents collected. Nests were labelled to avoid pseudo-replication and to

73   avoid resampling from chicks. The animal procedures used in this this study were reviewed and

74   approved by the Joint British Antarctic Survey - Cambridge University Animal Welfare and Ethical

75   Review Committee. Permits to operate were issued by the Government of South Georgia and the

76   South Sandwich Islands.

77   Sample B- bolus from an adult Grey-headed Albatross *Thalassarche chrysostoma* (Forster)

78   collected following Alvito et al. (2015). Bolus, regurgitated by an adult grey headed albatross that

79   had recently arrived at the colony was collected from the ground during a daily visit to the nesting

80   site.

81   The lower rostral length of the squid beaks was 13.4 mm (sample A) corresponding to 478

82   mm ML and 2545 g BW, and 9.2 mm (sample B) corresponding to 320 mm ML and 778 g BW

83   according to the allometric equations of Xavier and Cherel (2009).

84   Both bunches of spermatophores and spermatangia (ejaculated spermatophores) with

85   associated empty tunics were preserved first in 4% formalin and then transferred into 70% ethanol.

86   Total length was measured to the nearest 1 mm in all undamaged spermatophores and empty

87   envelopes. More detailed morphometric features were measured (to 0.1 mm) for a subsample of 27

88   spermatophores (sample A) and 25 spermatophores (sample B) under a Leica MZ 125 binocular

89   microscope.

90   **Results**

91   The reproductive system of the first *K. longimana* (sample A) consisted of remnants of the

92   spermatophoric sac that contained a total of 27 intact spermatophores, and 88 empty tunics (56 of

93   which were undamaged) left after spermatophore ejaculation. These envelopes were accompanied

94   by 30 spermatangia and some amorphous pieces of those without a normal spermatangial structure.

95   In this sample, the spermatophore length (SL) varied from 63–90 mm (Fig. 1, 2), mostly being 65–70

96   mm. Empty envelopes were 57–79 mm long. The seminal reservoir (SR) occupied more than a half of

97   the SL (Table 1), with a very small rear empty part behind it. SR was tight and occupied all available

98   space inside the spermatophore envelope behind the cement body. The cement body was

99   homogenous, closely attached to the seminal reservoir, without a distinctive separation from the

100 spiral filament of the ejaculatory tube. The head was distinctive, with about two loops of the spiral

101 filament inside and a strong thick thread. Spermatangium length varied from 26–60 mm, of which

102 17–38 mm were represented by a bulky, stick-like body, and the rest consisted of a long trailing tail

103 of inner envelopes.

104   The reproductive system from sample B contained an intertwined pack of spermatophores

105 (N=62, of which 54 were measurable) and empty envelopes (N=50, of which 37 were measurable).

106 Spermatophores were smaller, as expected for a smaller male (Fig. 2). Their morphology was

107 identical to that described above, and the morphometry was very similar (Table 1): SL ranged from

108 42–69 mm (mostly 55–65 mm), and the empty envelopes were 38–68 mm long.

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110 **Discussion**

111   Seabirds often forage on spent Antarctic deep-sea cephalopods that float up after spawning

112 is well known (Lininski and Jackson 1989; Croxall and Prince 1994; Cherel and Weimerskirch 1999;

113 Xavier et al. 2013). Indeed, rising to the surface after spawning is a common fate of females of many

114 meso- and bathypelagic squid (e.g. Onychoteuthidae, Gonatidae, Histioteuthidae and Cranchiidae)

115 that undergo gelatinous degeneration during maturation, and may explain the common occurrence

116 of large deep-water squids in the stomachs of seabirds, including those incapable of diving (Nesis et

117 al. 1998; Xavier et al. 2013). To our best knowledge, maturing and mature squid of the family

118 Onychoteuthidae were never reported from surface layers, where they could be available to

119 seabirds, as during maturation they descend into deep-sea well before become able to reproduce

120 (Arkhipkin and Nigmatullin 1997, Laptikhovsky et al. 2007). In contrast to this, spent male and

121 female onychoteuthids were regularly found floating at the surface (e.g. Clarke 1966; Arkhipkin and

122 Nigmatullin 1997; Bolstad and Hoving 2011 and references within). There is no trawl fishery around

123 South Georgia to suggest that these two males of *K. longimana* might be captured from deep-seas

124 and then discarded by fishermen though we cannot exclude a sheer theoretical possibility of

125 capturing these squid by two longliners operating in the area. However, throughout the entire

126 longlining history, which is closely monitored by observers onboard it occurred just once

127 (Laptikhovsky et al. 2013). Therefore we think that the possibility of these *K. longimana* being

128 brought up to the surface otherwise but by post-spawning body degeneration is highly unlikely.

129   The spermatophores of *K. longimana* in our study looked normal and were functional, as

130 they had ejaculated following the albatrosses' predation. They were very dissimilar to those of other

131 spent squid, in which the spermatophores have short, thin, semi-transparent, seminal reservoirs and

132 a progressively increasing rear empty part, as reported in senescent male oceanic squid *Illex*

133 *argentinus* (Laptikhovsky and Nigmatullin 1992) and *Gonatus antarcticus* (V. Laptikhovsky,

134 unpublished), following a gradual decline in testis activity. Rigid and dense seminal reservoirs

135 occupied 42–72% SL (mostly ca. 55–60% SL) in *K. longimana* and looked as those in other large cold-

136 and temperate water onychoteuthids, including *Onykia robsoni* (~ 70% SL), *O. robusta* (62–78% SL),

137 *O.ingens* (38–51% SL) and *Onychoteuthis borelijaponica* (66–70% SL), though they were longer than

138 reported in tropical and subtropical representatives of the family: *Onychoteuthis banksi* and

139 *Ancistroteuthis lichtensteini* (9–33%) (Hess 1987; Laptikhovsky 1990; Hoving et al. 2016). The SR of

140 *Kondakovia* had similar proportions to other Antarctic squids from other families, such as

141 *Galiteuthis glacialis* (42.4% SL) and *Mesonychoteuthis hamiltoni* (72.6–85.4% SL) (Hess 1987).

142 Numerous empty envelopes and spermatangia indicated that the spermatophores of male

143 *Kondakovia* foraged by albatrosses may have been ejaculated.

144   Our results show that in moribund male *K. longimana* the spermatophoric sacs contained at

145 least a hundred normal spermatophores and there was no evidence of malfunctioning of the

146 reproductive system. We might suppose that senescence processes in both sexes of *K. longimana*

147 occurs together with morphological and physiological changes in the mantle leading to spent and

148 partially spent individuals rising to the surface, as has been recorded in large polynyas in the

149 southern Indian Ocean, Ross Sea and Scotia Sea (Lu and Williams 1994; Vacchi et al. 1994; Lynne and

150 Rodhouse 2002). If such as process would occur faster than full degeneration of the reproductive

151 system, a male might die or lose neutral buoyancy before being fully spent. It is noticeable that the

152 beaks of senescent *K. longimana* (darkened wings, n=72) sampled from the diet of wandering

153 albatross belonged to animals with mode of 435 mm ML (Cherel and Weimerskirch 1999), which is

154 much smaller than the maximum reported size of immature females. Possibly, the buccal masses of

155 adult females are too big for albatrosses to swallow, and this part of the body may be more prone to

156 seabirds foraging.

157   Analysis of existing information allows to conclude that senescent male *K. longimana* are

158 320-480 mm ML (0.8 – 2.5 kg BW) mm and are thus about 1/10 the weight of senescent females (7-

159 29 kg or more), emphasising the sexual dimorphism of this species. Generally, males of medium-

160 sized and large nectonic oceanic oegopsid squid are either of the same size as females as noted in

161 the Thysanoteuthidae (Nigmatullin et al. 1995), or are slightly smaller than females, whereby the

162 maximum reported ML for males is about 70–85% of the maximum reported female ML (and

163   approximately half the body mass), as reported in Ommastrephidae, Gonatidae, Architeuthidae and

164   Onychoteuthidae (Filippova et al. 1997; Jereb and Roper 2010; Hoving et al. 2004, 2015). Only in

165   *Sthenoteuthis* and *Ommastrephes* (Ommastrephidae) are females 1.5-2 times larger and 2-5 times

166   heavier than males (Zuev et al. 2002; Jereb and Roper 2010).

167   The possible reason of extreme sexual dimorphism in *K. longimana* (~10 times difference in

168   weight between males and females) is the need to maximise reproductive output by channelling

169   most of the available resources into female somatic and generative growth in food – restricting

170   environment. On the other hand, a broad spectrum of adult size allows for a wider size spectrum of

171   prey (as do smaller squid hunt smaller fish), so potentially reducing intraspecific competition and

172   enhancing available trophic resources.

173   Our data also show that male *K. longimana* have extended spermatophore production, as

174   other squids and in contrast to that supposed by Clarke (1980). Spermatophore production in this

175   species likely lasts to the very last moment of life, and the bimodal spermatophore size structure

176   noticed by Clarke (1980) could be the result of males producing them seasonally and living for

177   several years, as female do.

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Figure captions:

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278 Figure 1. Detailed illustration of the spermatophore of *Kondakovia longimana*. A – the
279 spermatophore, B – spermatophore head, C – end of the cement body (an expansion of inner tunics
280 around the beginning of ejaculatory tube is not always present). Scale bars 1 mm.

281 Figure 2. Length-frequency distributions of spermatophores both intact and empty envelopes: A-
282 sample A, B – sample B.

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