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Life cycle of Chokka squid Loligo reynaudii in South African waters

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Published in:

African Journal of Marine Science

DOI:

[10.2989/1814232X.2016.1230074](https://doi.org/10.2989/1814232X.2016.1230074)

Publication date:

2016

Citation for published version (APA):

Lipinski, M., van der Vyver, F., Shaw, P. W., & Sauer, W. H. H. (2016). Life cycle of Chokka squid *Loligo reynaudii* in South African waters. *African Journal of Marine Science*, 38(4), 589-593 .
<https://doi.org/10.2989/1814232X.2016.1230074>

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26 **Introduction**

27

28 The life cycle of the chokka squid (*Loligo reynaudii* D'Orb., 1848) has been debated in a
29 number of publications (e.g. Augustyn 1989; Augustyn et al. 1992, 1994; Oylott et al. 2006,
30 2007; Sauer et al. 2013; van der Vyver et al. 2015). The first three accounts came up with a
31 simple biological scheme. This scheme, set out in Figure 1 and Figure 2, was based primarily
32 on biological analyses during research conducted on both commercial vessels and the
33 Fisheries Research Vessel "Africana" from 1983 onwards.

34 In the distribution terms, main spawning areas were detected and mapped (e.g. Sauer et al.
35 1992) inshore between Plettenberg Bay and Port Alfred. Other spawning grounds, although
36 detected and mentioned in various publications, were considered minor. Paralarvae were
37 mainly detected around spawning grounds, but were present along the whole south coast
38 (Augustyn et al. 1994). Paralarvae detected along the west coast were identified (Vecchione
39 & Lipinski 1995) as *Afrololigo mercatoris* (Adam, 1941).

40 Juveniles of 20-80 mm ML were mainly detected between Plettenberg Bay and Cape
41 Agulhas, although they were present year round along the whole south coast. Adult squid
42 which were usually detected offshore hunting in small schools all over Agulhas Bank, were
43 thought to return in their bulk to main spawning grounds, and the whole cycle will repeat
44 itself (Augustyn et al. 1994).

45 Figure 2 fills some details of the scheme illustrated on Figure 1. According to this scheme,
46 most of the squid spawns in the east, all paralarvae drift to the common paralarval pool (from
47 which some hypothetically drift to the west coast and grow, but most of these get lost). One
48 stock of squid, recruited from this paralarval pool, feeds and grows on the Agulhas Bank.
49 Some part of it spawns locally inshore (short migration), some migrate to the west coast
50 waters, but most return eastward to spawn.

51

52 More thorough analysis of the existing data (summarized in Augustyn et al. 1994) and then
53 additional analyses of old and new data (e.g. Olyott et al. 2006, 2007) supplemented this
54 established view. Most important points of departure were as follows:

- 55 1. There is unquantified spawning of *Loligo reynaudii* in deep waters (deeper than 70 m;
56 Augustyn et al. 1994; Roberts & Sauer 1994);
- 57 2. Juveniles 20-80 mm are much wider distributed along the south coast, highest
58 densities of them are detected between Algoa Bay and Cape St. Francis, slightly
59 offshore in relation to their spawning grounds (Augustyn et al. 1994);
- 60 3. Migrations of adults between Tsitsikamma and Port Alfred indeed take place up to
61 200 km, they mainly in west to east direction but are complicated and interpretation of
62 emerging patterns is difficult. Each spawning concentration is very dynamic;
63 exchange there may be 0.2 of its biomass per day, or more (Lipinski et al. 1998; Sauer
64 et al. 2000).

65 **Results and Discussion**

66 New evidence

67 More recently a combination of ecological, morphological, environmental and genetic
68 research has questioned our understanding of the life cycle of chokka, calling for more
69 complicated structure than first envisaged (Shaw et al. 2010, Sauer et al. 2013; van der Vyver
70 et al. 2015), however, the published accounts of these findings stopped short of providing a
71 new life cycle scheme of chokka squid, which is the aim of the present note.

72

73 The following new facts and interpretations were become available:

- 74 1. Spawning in the deep was confirmed, mapped and quantified as having 18% share in
75 total spawning. Ecological experiments have proven the viability of this spawning as
76 producing healthy hatchlings (Oosthuizen & Roberts 2009; Roberts et al. 2012).
- 77 2. Simulation experiments pointed out to complicated distribution of paralarvae and
78 possible substantial losses during their drift (Roberts & Mullon 2010).
- 79 3. Scarcity, but constant presence of chokka between St. Helena Bay and Kunene River
80 was confirmed (Lipinski unpublished results of R/V Dr Fridtjof Nansen cruises).
- 81 4. Separate but viable sub-population of chokka in the southern Angola (up to 500 km
82 from Kunene) is the object of some artisanal fisheries. Mature squid were noted there,
83 but nothing is known about egg beds and paralarvae (van der Vyver 2015; Sauer
84 unpublished results).
- 85 5. As the result of genetic and morphometric studies it was found that there is little
86 genetic diversity even between most distant sub-populations (Angolan vs. Port
87 Alfred). However, morphometric diversity was significant between south coast of SA,
88 western Agulhas and west coast of SA, and Angola (van der Vyver 2015; Fig. 3). This
89 regional patterns of morphological divergence observed, occurred against a backdrop
90 of high gene flow, which was interpreted as the influence of environmental
91 heterogeneity and not genetic drift/isolation as the primary driver of the phenotypic
92 differences. The observed phenotypic heterogeneity probably reflects the interplay
93 between genetic adaptation and short term plasticity, which may vary throughout the
94 geographic range of the study, and be a start of more profound morphological
95 differences (e.g. in beaks or statoliths) and then stable genetic differences. The
96 existence of the three morphological domains (Eastern and Central Agulhas, Western
97 Agulhas and West Coast, and southern Angola) calls for further revision of the

98 existing life cycle on a geographic and temporal background, especially when more
99 biological data will become known about Angolan population.

100

101

102 Life cycle as known today (2016) is presented on the Figures 3-4 as follows.

103 *Loligo reynaudii* forms mobile, large metapopulation. Most northern (Angolan) part of this

104 metapopulation is not genetically isolated from other, southerly components, but differs

105 morphologically. Since mixing with nearest abundant group (St. Helena – Western Agulhas)

106 is minimal due to scarcity of individuals over nearly 1800 km of coastline, this Angolan sub-

107 population is likely to be a recent extension of the species range northwards, and has its own

108 breeding and paralarval transport regime. Morphological differences between west coast plus

109 Western Agulhas, and Eastern Agulhas plus Tsitsikamma – Port Alfred are maintained

110 throughout two different paralarval pools, which are further divided into the smaller groups.

111 Deep water spawning, on the other hand helps to maintain relative homogeneity of this part

112 of the meta-population (exclusively South African), as is migration in space and time (i.e.

113 subsequent generations in different areas, as changing environment will dictate). Migration of

114 adult squid is generally short (around 200 km) and may proceed in all directions, including

115 inshore – offshore (Sauer et al. 2000). Hypothetical long migration may exist on a small

116 scale, although it was never documented. There also may be some adult squid which does not

117 migrate at all, but again this has not been documented.

118

119 This life cycle scheme differs sharply with the first simple proposal. The latter superficially

120 agrees well with the genetic results of van Vyver et al. 2015, but not with morphological part

121 of their study. Observed morphological differences have to be rooted in the early

122 development (on a paralarval stage). This in turn may be related with timing of hatching

123 during the year, transport of paralarvae, their survival and their final destination, and
124 subsequent small movements of juveniles on their nursery grounds. It is hoped that proposed
125 scheme (Figs. 3-4) reflects well this biological reality.

126

127 **Funding and Ethical Considerations**

128

129 This note does not provide information about new data – all data were already collected
130 under various programs and acknowledged in publications cited in this note. This note is
131 about new idea concerning the life cycle of squid and the only cost is the time spent by
132 authors during writing it – no specific funding was obtained. This note does not contain any
133 studies with animals performed by any of the authors. There is no conflict of any interests
134 whatsoever.

135

136 **Acknowledgements**

137

138 Many of our colleagues from the Department of Agriculture, Forestry and Fisheries, from the
139 Department of Environmental Affairs, from the Rhodes University and from the South
140 African Squid Management Industrial Association (SASMIA) helped in various ways over
141 years. They deserve our gratitude.

142

143

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195

196 **Figure Legends**

197

198 **Fig. 1.** The scheme of geographic distribution and movement of paralarvae and adults of
199 chokka squid (*Loligo reynaudii*), as understood in the early years of research.

200

201 **Fig. 2.** The life cycle of chokka squid, according to distributional scheme illustrated on Fig.
202 1. There are two clusters of spawning sites: main off the Eastern Cape, and accessory off the
203 Western Agulhas coast. There is only one paralarval pool, fed along similar routes throughout
204 the year but mainly in November-December. Thick arrows indicate main circulation in the
205 life cycle scheme; thinner arrows indicate supplementary processes. Broken lines indicate
206 paralarval movements. Size of rectangular boxes represent approximate strength of each
207 migration event. Lost paralarvae were, as many larvae of other species, a result of being
208 carried away from coast by the Agulhas Current and its offshoots. It is unclear if any
209 paralarvae reach the west coast (marked by question marks).

210

211 **Fig.3.** A revised representation of the geographic distribution of chokka:.(A) west coast of
212 southern Africa; (B) south coast of South Africa.

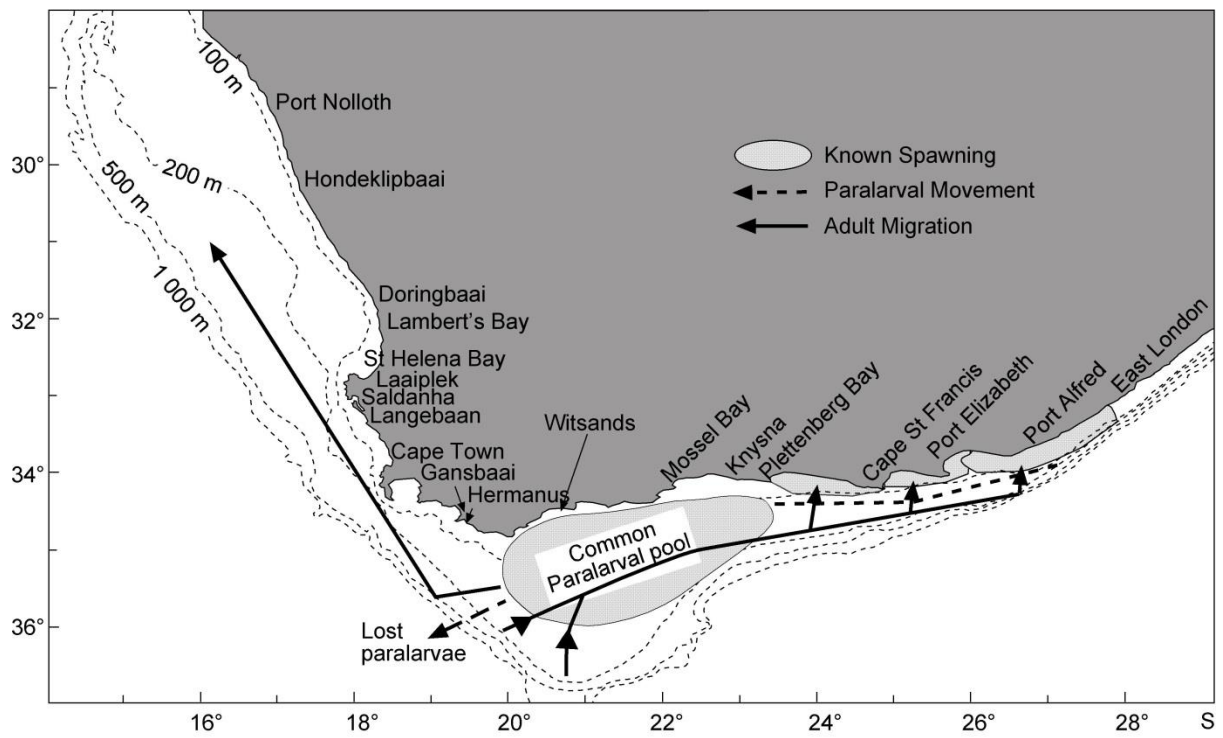
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214 **Fig. 4.** New life cycle scheme of chokka. There are three blocks of information: Angola,
215 where very little data is available; Eastern Agulhas and Eastern Cape spawning grounds; and
216 Central and Western Agulhas spawning grounds. Last two also include deep water spawning
217 grounds. Main departure from the previous scheme is a partition of one large paralarval pool
218 into separate paralarval “events” which are different in space, time, or both. Also, possible
219 loss of paralarvae was documented from both Eastern Agulhas and Western Agulhas (Roberts
220 and Mullon 2010). Thick arrows indicate main circulation in the life cycle scheme; thinner

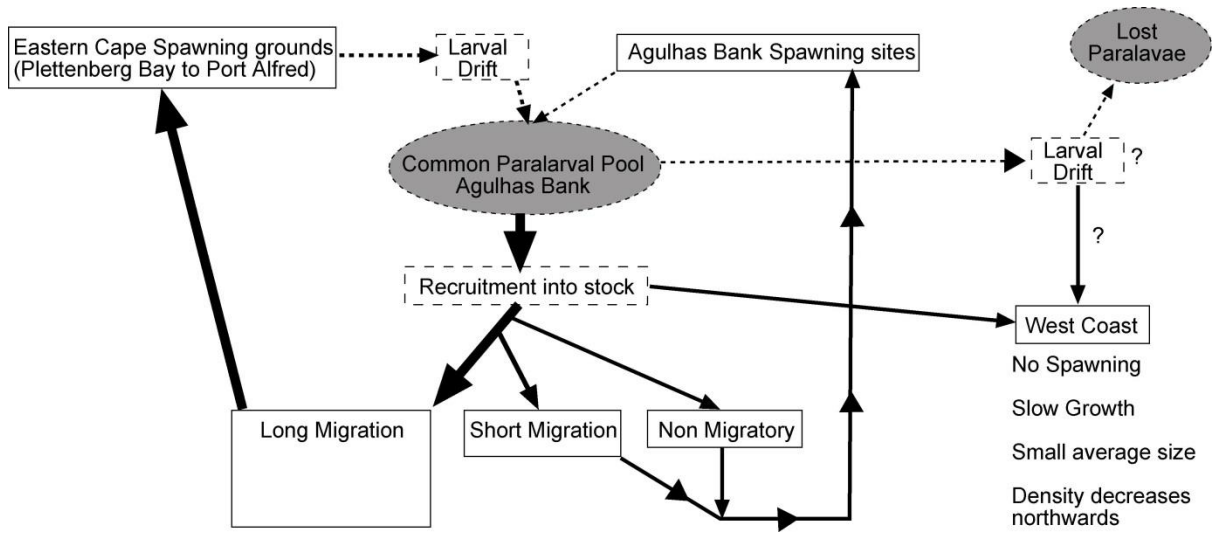
221 arrows indicate supplementary processes. Broken lines indicate paralarval movements. Size
222 of rectangular boxes represent approximate strength of each migration event. It is unclear if
223 any paralarvae reach the west coast (marked by question marks).

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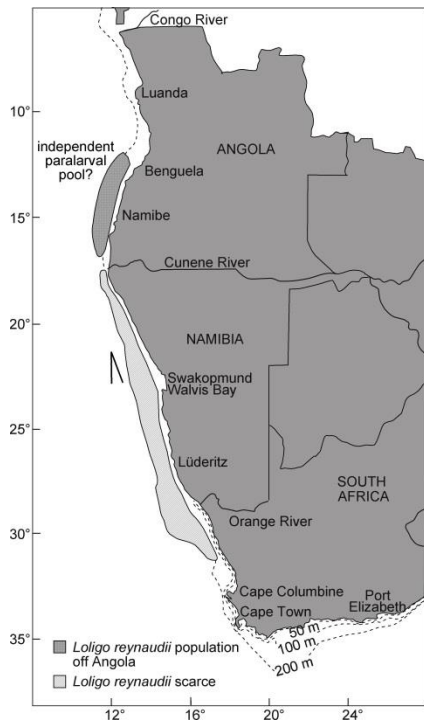


226
227 Fig. 1
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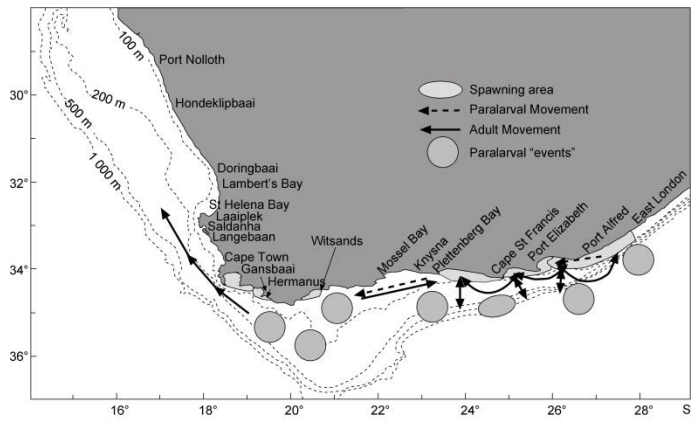
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Fig. 2



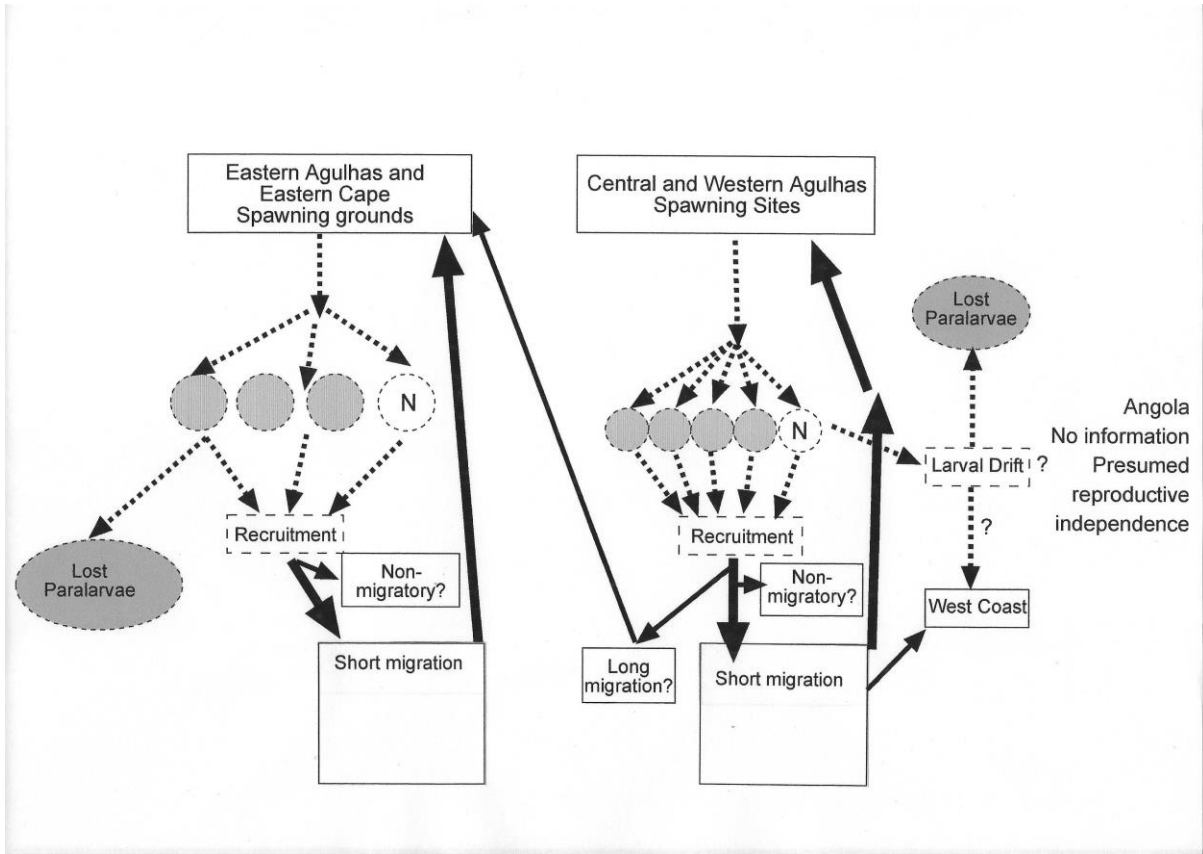
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Fig. 3A



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Fig. 3B



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Fig. 4