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LIFE CYCLE OF CHOKKA SQUID, *LOLIGO REYNAUDII*

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Abstract

This short note summarizes past and present knowledge about life cycle of chokka squid *(Loligo reynaudii* D'Orb., 1848*).* In the past (until about 2010) chokka stock was considered simple and uniform, with one paralarval pool, drift of palararvae westwards, one main nursery area and one main long spawning migration of adult squid eastwards, back to the main spawning grounds. New findings revised this life cycle. Although genetically the stock is uniform, but morphologically it comprises three main geographic groups. It is proposed that their differences originate from many different palaralval "events", and that short (not long) migrations dominate the life cycle.

Keywords: life cycle, Loligo reynaudii, squid.

Introduction

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

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

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

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

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

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

Results and Discussion

New evidence

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

The following new facts and interpretations were become available:

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

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

Life cycle as known today (2016) is presented on the Figures 3-4 as follows.
Loligo reynaudii forms mobile, large metapopulation. Most northern (Angolan) part of this metapopulation is not genetically isolated from other, southerly components, but differs morphologically. Since mixing with nearest abundant group (St. Helena – Western Agulhas) is minimal due to scarcity of individuals over nearly 1800 km of coastline, this Angolan sub-population is likely to be a recent extension of the species range northwards, and has its own breeding and paralarval transport regime. Morphological differences between west coast plus Western Agulhas, and Eastern Agulhas plus Tsitsikamma – Port Alfred are maintained throughout two different paralarval pools, which are further divided into the smaller groups. Deep water spawning, on the other hand helps to maintain relative homogeneity of this part of the meta-population (exclusively South African), as is migration in space and time (i.e. subsequent generations in different areas, as changing environment will dictate). Migration of adult squid is generally short (around 200 km) and may proceed in all directions, including inshore – offshore (Sauer et al. 2000). Hypothetical long migration may exist on a small scale, although it was never documented. There also may be some adult squid which does not migrate at all, but again this has not been documented.

This life cycle scheme differs sharply with the first simple proposal. The latter superficially agrees well with the genetic results of van Vyver et al. 2015, but not with morphological part of their study. Observed morphological differences have to be rooted in the early development (on a paralarval stage). This in turn may be related with timing of hatching during the year, transport of paralarvae, their survival and their final destination, and subsequent small movements of juveniles on their nursery grounds. It is hoped that proposed scheme (Figs. 3-4) reflects well this biological reality.

Funding and Ethical Considerations

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

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Figure Legends

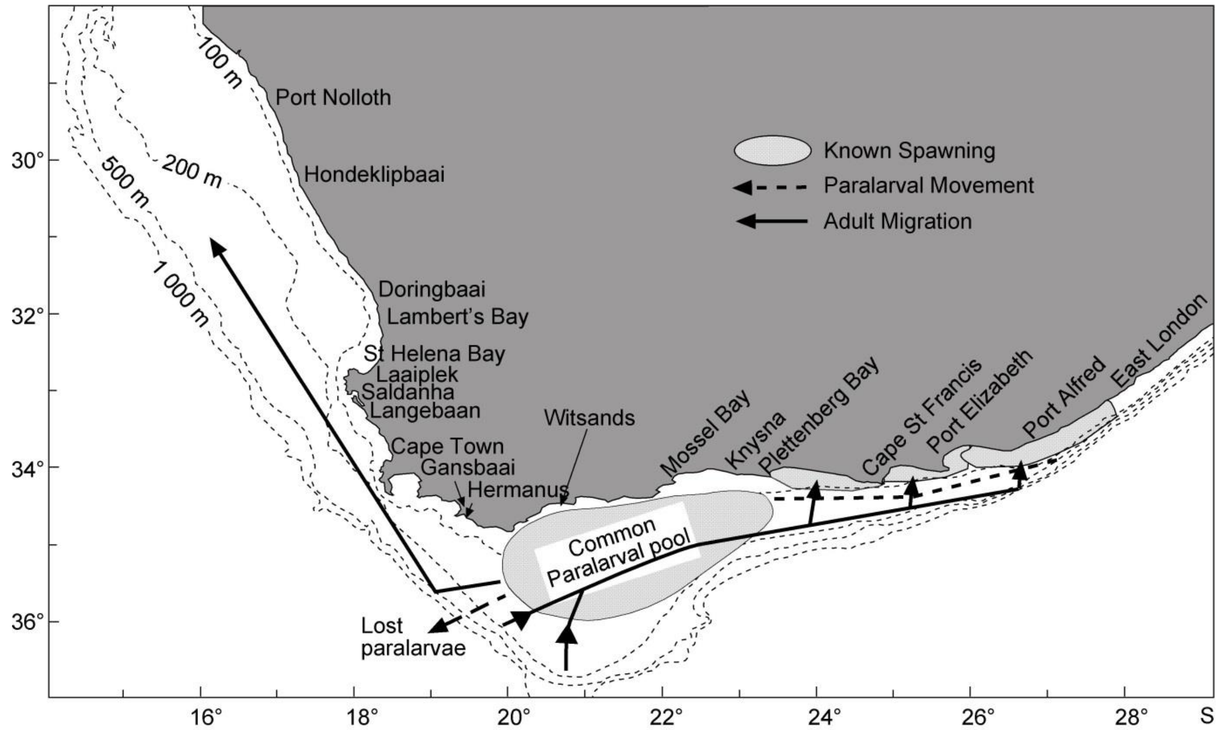
Fig. 1. The scheme of geographic distribution and movement of paralarvae and adults of chokka squid (*Loligo reynaudii),* as understood in the early years of research.

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

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

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

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


100 m
200 m
500 m
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Port Nolloth
Hondeklipbaai
Doringbaai
Lambert's Bay
St Helena Bay
Laaiplek
Saldanha
Langebaan
Cape Town
Gansbaai
Hermanus
Witsands
Mossel Bay
Knysna
Plettenberg Bay
Cape St Francis
Port Elizabeth
Port Alfred
East London
Known Spawning
Paralarval Movement
Adult Migration
Common Paralarval pool
Lost paralarvae
30°
32°
34°
36°
16°
18°
20°
22°
24°
26°
28°
S

Fig. 1

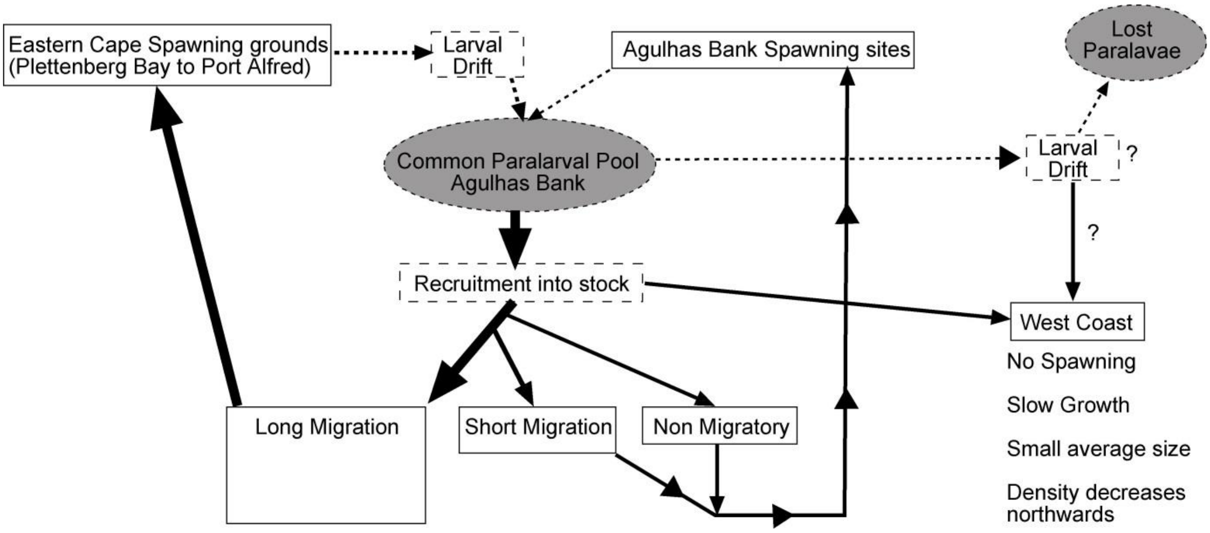
Eastern Cape Spawning grounds
(Plettenberg Bay to Port Alfred)
Larval
Drift
Agulhas Bank Spawning sites
Lost
Paralavae
Common Paralarval Pool
Agulhas Bank
Larval
Drift
?
?
Recruitment into stock
West Coast
No Spawning
Slow Growth
Small average size
Density decreases
northwards
Long Migration
Short Migration
Non Migratory

Fig. 2

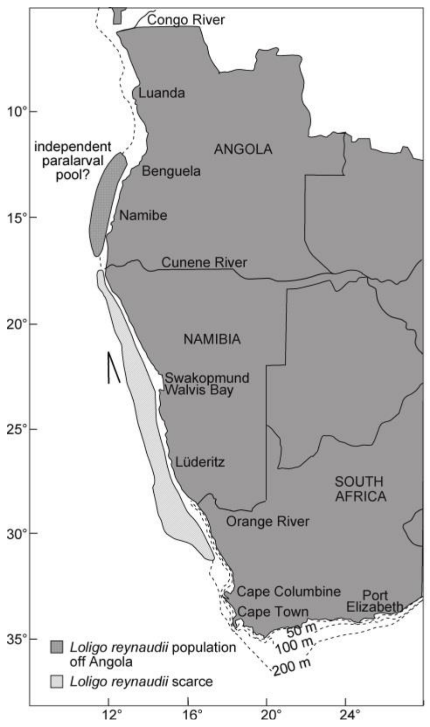
Congo River
Luanda
10°
independent paralarval pool?
ANGOLA
Benguela
15°
Namibe
Cunene River
20°
NAMIBIA
Swakopmund
Walvis Bay
25°
Lüderitz
SOUTH AFRICA
Orange River
30°
Cape Columbine
Port Elizabeth
Cape Town
50 m
100 m
200 m
35°
Loligo reynaudii population off Angola
Loligo reynaudii scarce
12°
16°
20°
24°

Fig. 3A

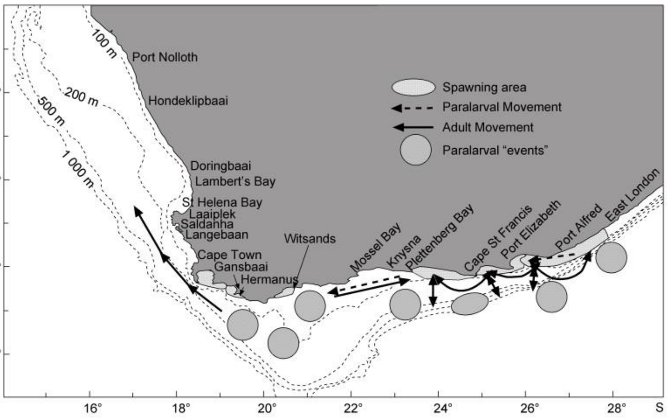
Port Nolloth
Hondeklipbaai
Doringbaai
Lambert's Bay
St Helena Bay
Laaiplek
Saldanha
Langebaan
Cape Town
Gansbaai
Hermanus
Witsands
Mossel Bay
Knysna
Plettenberg Bay
Cape St Francis
Port Elizabeth
Port Alfred
East London
100 m
200 m
500 m
1 000 m
Spawning area
Paralarval Movement
Adult Movement
Paralarval "events"
30°
32°
34°
36°
16°
18°
20°
22°
24°
26°
28°
S

Fig. 3B

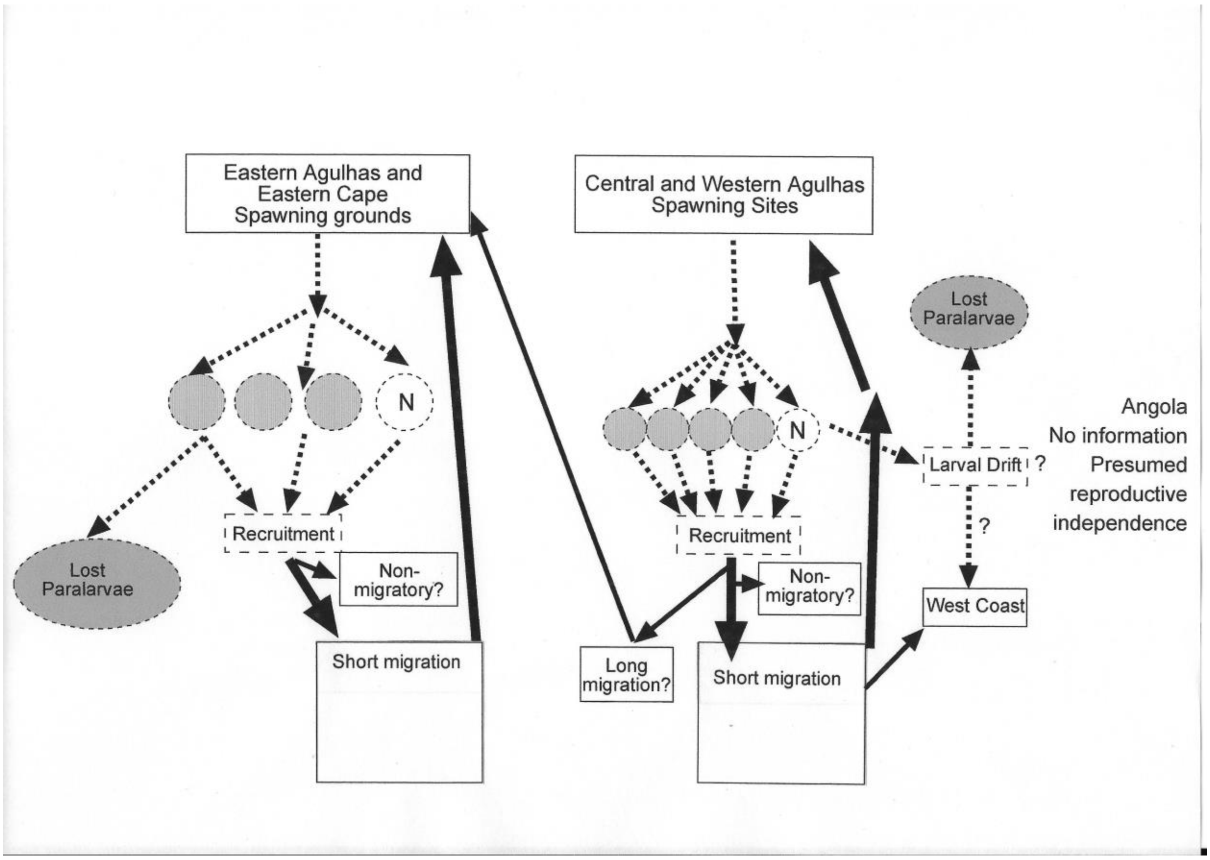
Eastern Agulhas and Eastern Cape Spawning grounds
Central and Western Agulhas Spawning Sites
Lost Paralarvae
N
Recruitment
Non-migratory?
Short migration
Lost Paralarvae
N
Larval Drift ?
Angola
No information
Presumed reproductive independence
?
Recruitment
Non-migratory?
West Coast
Long migration?
Short migration

Fig. 4