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# Chokka squid on the Agulhas Bank: life history and ecology

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*Available knowledge is reviewed and new data incorporated in a synthesis of the life history and ecology of the chokka squid *Loligo vulgaris reynaudii*. We attempt to show that these aspects are essential to rational management of the resource. The life cycle is described in detail from the egg to adult stage, mainly in biological terms, including a comprehensive description of maturation, migration and reproduction. Possible ecological interactions, particularly those of paralarvae and copepods, are discussed. Predator-prey relationships and the current state of knowledge on the effect of the physical environment on squid availability and abundance are summarized.*

The chokka squid *Loligo vulgaris reynaudii* is the subject of one of the most valuable fisheries based on the South African south coast, providing employment for about 2 500 fishermen and over 1 000 land-based workers and other personnel. The fishery, its history and management has recently been described in detail by Augustyn *et al.*<sup>1</sup> and Sauer.<sup>2</sup>

Squid fisheries are notoriously difficult to manage; population levels and availability can change drastically without warning.<sup>3,4</sup> These fluctuations have been ascribed to fishing pressure,<sup>5</sup> natural variations<sup>4,6</sup> or both. Fisheries based on loliginid squids tend to be more stable than those based on ommastrephids.<sup>7,8</sup> Despite this, few loliginid fisheries are managed to any degree. The absence of a management strategy for the chokka fishery is highly risky,<sup>1</sup> because exploitation occurs largely on the spawning grounds\* and recruitment is highly dependent on complex interactions, including environmental factors. Augustyn *et al.*<sup>1</sup> point out, however, that rational, but not necessarily optimal, management decisions can be made in the absence of reliable fisheries models such as stock recruitment relationships, by the employment of common-sense measures which generally include some form of effort control.

Chokka squid is a key component in the Agulhas Bank ecosystem<sup>9</sup> and knowledge of its predator-prey relationships with other organisms in the region has value for the management of both the chokka squid and other resources, such as pelagic fish prey and marine mammal and linefish predators.

Table 1 presents a summary of publications to date on chokka squid. Knowledge has accumulated rapidly in recent years as a fully fledged research programme has been developed, leading to an improved understanding of the dynamics of the stocks.

The emphasis of the present review is on the usefulness of knowledge of the life history in managing the resource. This is the first attempt at summarizing this knowledge, and includes descriptions of population structure, distribution, abundance and recruitment trends, a detailed synthesis of what is known about life-cycle stages in terms of both morphology and reproductive biology, as well as a review of ecological influences, including trophic relationships and the physical environment.

\*'Spawning grounds' refers to the jig fishing grounds, generally shallower than 50 m, whereas 'shelf' refers to the rest of the species' range to approximately 300 m.

## Life history

### Population structure and distribution

Population structure has been examined over the distributional range of chokka squid at various times of the year.<sup>10-16</sup> These studies have enabled hypotheses on immigration patterns and population cohorts to be constructed. On the south coast,<sup>†</sup> three main size groups are evident at any time of the year, though the largest is only a remnant in autumn and winter on the shelf. In autumn the size structure is dominated by recruits, which originate from the summer peak spawning period. In spring, the juvenile cohort is much less dominant and there is a

Table 1. Publications to date on *Loligo vulgaris reynaudii*.

Reference	Year	Subject
Badenhorst <sup>82</sup>	1974	Male reproductive morphology
Hatanaka <i>et al.</i> <sup>10</sup>	1983	S. coast abundance, population structure, basic reproductive biology (summer)
Uozumi <i>et al.</i> <sup>11</sup>	1984	S. coast abundance, population structure, basic reproductive biology (winter)
Uozumi <i>et al.</i> <sup>12</sup>	1985	Description of jig fishery
Augustyn <sup>17</sup>	1986	SE coast food and feeding
Lipiński <sup>59</sup>	1987	Biochemical and morphological systematics
Augustyn & Grant <sup>18</sup>	1988	Systematics, life cycle and fisheries potential
Augustyn <sup>13</sup>	1989	Resource description, life cycle summary
Augustyn & Smale <sup>83</sup>	1989	Jig fishery, spawning grounds population structure, reproductive biology, feeding
Augustyn <sup>14</sup>	1990	Feeding physiology (caecum pH)
Lipiński <sup>62</sup>	1990	Fishery and future perspectives
Lipiński <sup>84</sup>	1990	Biomass, predation by seals
Lipiński & David <sup>71</sup>	1990	Gonad histology
Sauer & Lipiński <sup>40</sup>	1990	W. coast abundance, population structure, reproductive biology, feeding
Augustyn <sup>16</sup>	1991	Spawning grounds population cycle, reproductive biology
Sauer <sup>15</sup>	1991	Sea temperature/spawning relationship
Sauer, Goschen & Koorts <sup>80</sup>	1991	Spawning grounds feeding
Sauer & Lipiński <sup>58</sup>	1991	Predation on spawning squid
Sauer & Smale <sup>69</sup>	1991	Management review and life-cycle summary
Augustyn, Lipiński & Sauer <sup>1</sup>	1992	Location of spawning grounds, spawning and shoaling behaviour
Sauer, Smale & Lipiński	1992	Stock assessment methods
Augustyn, Roel & Cochrane <sup>21</sup>	(1993)	Egg distribution and abundance
Sauer, McCarthy, Smale & Koorts <sup>22</sup>	(1993)	Spawning behaviour
Sauer & Smale <sup>42</sup>	(1993)	

<sup>†</sup>'South coast' refers to the shelf area between Cape Agulhas and Port Alfred, including the Agulhas Bank, whereas 'west coast' applies to Cape Agulhas to the Orange River.

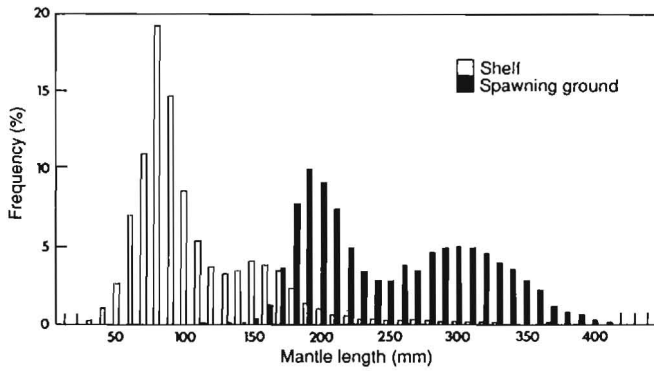


Fig. 1. Population size structure on the shelf (all data combined, from biomass surveys 1986–1992) compared with that on the spawning grounds (July 1988 to June 1989, from Sauer<sup>15</sup>).

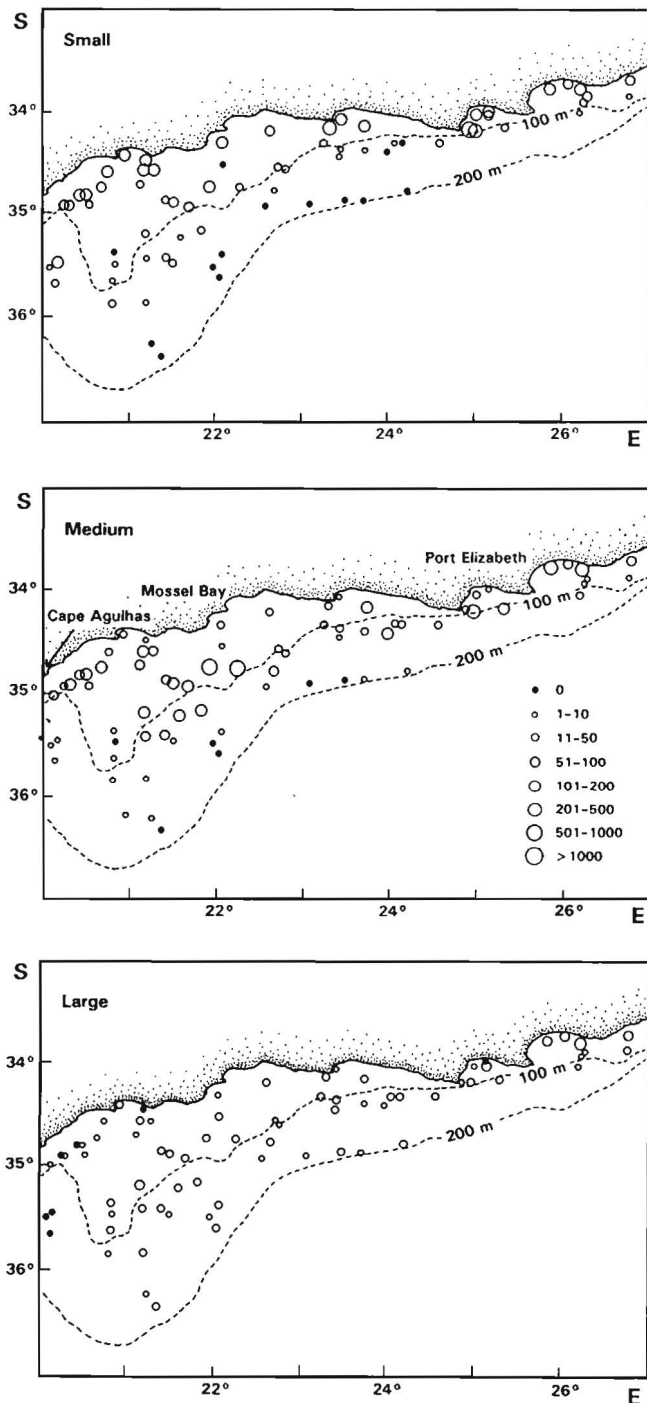


Fig. 2. Distribution of three size classes of chokka squid off the south coast, from a biomass survey in May 1992.

strong cohort of subadults peaking at about 145 mm. The main differences in population structure between the spring and autumn seasons are in the recruiting cohort and a slightly larger-sized adult cohort in autumn.

The proportion of adult stock is highest at depths of 101–200 m during both spring and autumn, whereas the proportion of juveniles is highest at 0–50 m. The 51–100-m depth range reflects the occurrence of intermediate-sized squid in spring whereas mainly juveniles occur there in autumn. The adult cohort on the spawning grounds is not adequately sampled by the biomass surveys. The year-round population structure of the spawning ground has been analysed in detail by Sauer and Augustyn (in prep.).

In autumn, prominent juvenile cohorts occur along the entire south coast. At this time, cohorts of larger animals are not dominant in any area. The east–west distribution is rather different in spring, with a very small cohort (35–75 mm) off the spawning grounds (25–26°E), larger juveniles prominent in the west, and cohorts of larger animals most prominent in the east.

The modal sizes of male and female squid on the spawning grounds are much larger than those sampled on the shelf,<sup>15</sup> and the population there is dominated by the largest cohort (Fig. 1).

Various aspects of the distribution of chokka squid have been discussed in earlier publications.<sup>1,13–16,17,18</sup> Early south-coast data, such as from the joint Japanese–South African surveys,<sup>10–12</sup> indicated general distributional trends, but did not cover the whole depth range adequately. New data, in the form of plots of numbers of squid per station in three size groups (Fig. 2), show distribution patterns over the whole depth range of their occurrence. These data confirm that small squid are distributed along the entire south coast, predominantly at depths of less than 100 m, the medium-size group is widely distributed slightly further offshore and the large adults are found mainly deeper than 100 m and also inshore in the east.

The west-coast squid population has been studied separately, mainly as a consequence of the Sea Fisheries Research Institute's demersal biomass surveys. Augustyn<sup>16</sup> showed that the distribution of squid there was continuous from the east and that a significant but highly variable part of the biomass often occurs off the west coast, to greater depths than on the south coast. The population consists mainly of immature and maturing subadults; few juveniles or large, mature animals are found there. The size distribution is generally unimodal. Feeding rates are higher than on the south coast. There is no direct evidence of spawning on the west coast north of Robben Island.

#### Biomass and recruitment trends

An index of biomass of squid on the south-coast shelf has been obtained using stratified random sampling on a regular basis since 1986. The methodology and limitations of these

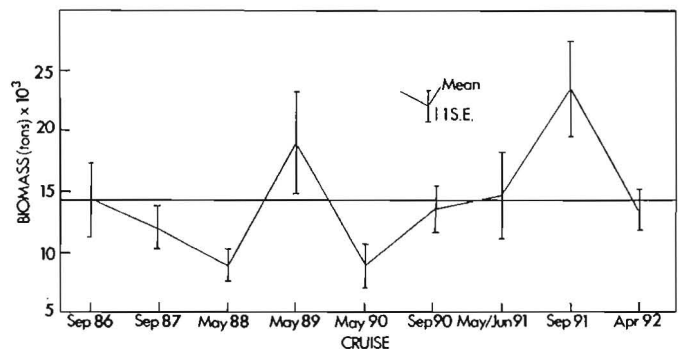


Fig. 3. Chokka squid biomass fluctuations on the south coast, as measured by SFR I stratified random-sampling surveys.

surveys have been discussed previously.<sup>1,13</sup> The latest results are presented in Fig. 3, which shows that biomass fluctuates generally by a factor of about 2.5.

Biomass levels on the west coast, as reflected in the indices from surveys there, tend to vary from almost zero to relatively high levels. These fluctuations have been attributed to immigration to, and emigration from, the area during the life cycle.<sup>16</sup>

To estimate the size of the highly aggregated spawning stock, a promising approach is that of hydro-acoustics, which is described by Hampton.<sup>19</sup> Jefferts *et al.*<sup>20</sup> have used this method to estimate spawning biomass of *Loligo opalescens*. Preliminary results on the feasibility of the method have been reported by Augustyn *et al.*<sup>21</sup>

Sauer *et al.*<sup>22</sup> have reported that it is possible to estimate the number of egg capsules present in an egg bed, using both random and non-random methods of dive transects. Once fecundity values are known, such egg-abundance estimates could be applied to the estimation of spawner biomass.

Augustyn *et al.*<sup>21</sup> also describe a modelling approach to squid stock assessment on the spawning grounds, using Leslie-Delury analyses, by means of which catch-per-unit-effort (CPUE) data are utilized to monitor stock performance. The aim of this model is the harvesting of a constant proportion of the stock and effort regulation. The implications of its use for squid stock management are discussed by Augustyn *et al.*<sup>1</sup>

#### The life cycle

Augustyn *et al.*<sup>1</sup> have succinctly described the life cycle of chokka squid in terms of various phases, namely hatching, followed by a passive planktonic phase, an active planktonic phase, migration to feeding grounds, attainment of maturity, migration to spawning grounds, mating and finally spawning. The following account attempts to be more comprehensive in describing the progression from egg stage to adult.

**Eggs.** The eggs of chokka squid (Fig. 4) are very similar to those of other loliginids, such as *L. opalescens*.<sup>23</sup> They are ovate, measuring about 2.8 mm long and 2.0 mm wide. They are yolky in appearance, the yolk being about 1.8 mm in length and 1.4 mm in width, and are arranged in a spiral within an elongated gelatinous capsule approximately  $86 \pm 14$  mm in length ( $n = 7$ ). A mean of  $110 \pm 16$  eggs were counted in a sample of six capsules.<sup>13</sup>

Early-stage egg capsules are smooth, gelatinous, elongated, bright orange in colour, and transparent, the eggs being clearly visible. During development of the embryos, the colour slowly changes to a browner hue, and the capsule takes on a knobbed

appearance as water is absorbed. Egg capsules are attached by stalks, the basal ends of which form a gelatinous, intertwined mass usually embedded in the substratum. Capsules joined in this way form clusters.

Clusters vary greatly in size, containing from single capsules to very large numbers. Augustyn<sup>14</sup> has described a large cluster consisting of 6 700 capsules. Egg beds typically consist of a large central bed (in some cases at least 6 m in diameter) with smaller clusters surrounding it, and single egg capsules in the immediate vicinity. These spawning locations are non-randomly distributed along the inshore south-eastern Cape coastline.<sup>21,24</sup>

The basic outline of embryogenesis in cephalopods, much of which is also applicable to chokka squid, is described by Naef<sup>25</sup> and Boletzky.<sup>26,27</sup> In *L. opalescens* it has been described in great detail by Fields;<sup>23</sup> in chokka squid by Blackburn and Sauer (in prep.). The eggs take approximately 35 days to hatch at 14°C and 16 days at 21–22°C. In a hatching experiment, eggs did not develop normally at temperatures below 10°C or above 24°C. (Augustyn *et al.*,<sup>1</sup> Fig. 7). Further experiments are in progress to confirm these findings. In *L. vulgaris vulgaris*, hatching takes 40–45 days at 12–14°C, about 30 days at 17°C and 26–27 days at 22°C,<sup>28,29</sup> in *L. pealei*, 27 days at 12°C and 10 days at 23°C.<sup>30</sup> Chokka squid eggs have an almost 100% hatching rate in the laboratory at 14–20°C (C.J.A., pers. obs.).

**Paralarvae.** Newly hatched chokka squid (which we shall refer to as paralarvae<sup>31</sup>) are not completely developed morphologically, the tentacles and arms being very small and not all easily visible (Fig. 5, also Blackburn and Sauer, in prep.). An external yolk sac is often still attached and the gut is still filled with yolk. The remains of the yolk sac normally break off at or soon after hatching. The hatchlings have enough yolk left in the gut to last about 4 days without food at about 12°C (C.J.A., pers. obs.). At hatching, paralarvae have a mean total length of  $4.67 \pm 0.22$  mm and a mean mantle length of  $2.33 \pm 0.18$  mm ( $n = 18$ ).<sup>13</sup>

Young paralarvae are not strong swimmers and lead a passive, planktonic existence.<sup>32–34</sup> In captivity they display an almost vertical posture, are negatively buoyant, and have to jet almost continuously to maintain their position in the water column.<sup>1</sup> It is not known at what size or age they begin to swim horizontally, but according to Mangold-Wirz<sup>28</sup> the duration of planktonic life is 2–3 months in *L. vulgaris vulgaris*.

The distribution of chokka squid paralarvae from Bongo net sampling between the years 1985 and 1991 is presented in Fig. 6. The size range of the paralarvae was 2–9 mm mantle

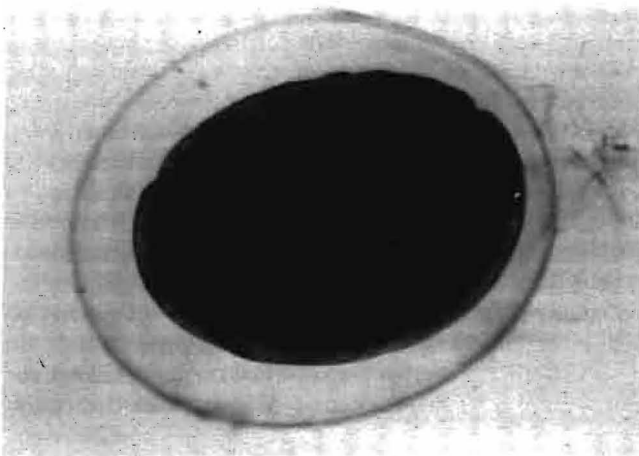


Fig. 4. Chokka squid ovum (length 2.80 mm).

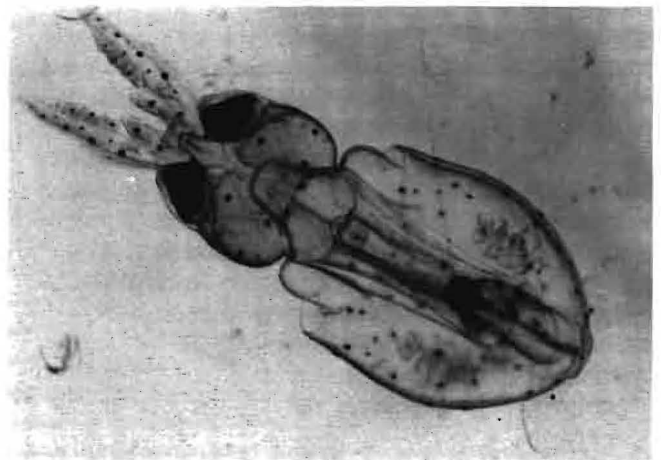


Fig. 5. Newly hatched chokka squid paralarva (ventral view).

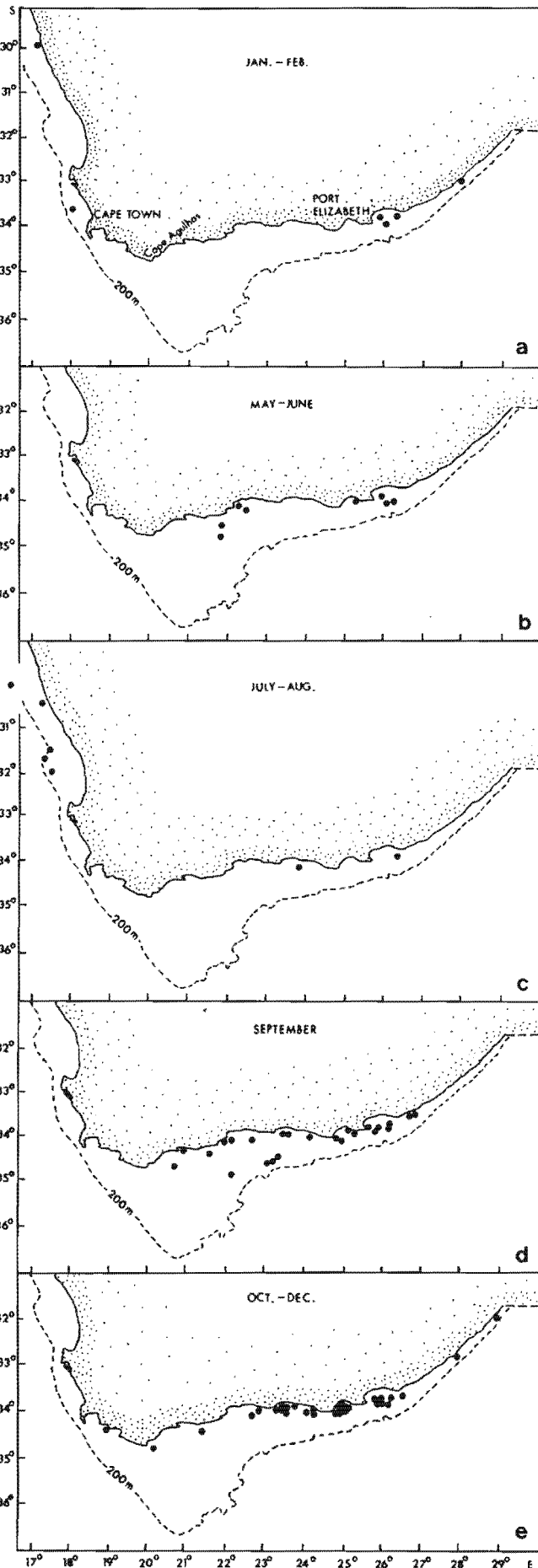


Fig. 6. Distribution of chokka squid hatchlings in South African waters, 1985-91. a, January/February; b, May/June; c, July/August; d, September; e, October to December.

length (ML), but most were 2-4 mm. Although not quantitative, these data agree with other sources that the main spawning and hatching period is from September to December, and that the main spawning region extends from about Algoa Bay to Plettenberg Bay but may be scattered as far as Great Fish Point in the east and Danger Point in the west. In other months of the year they are generally scarce, but widely dispersed: from East London to south of Port Nolloth on the west coast. Full results of the paralarval survey will be presented by Lipiński (in prep.).

**Juveniles.** As the young squid grows, the arms and mantle become much longer in relation to the head, and the fin becomes elongated, in the typical shape of loliginids. The characteristic paralarval chromatophore pattern<sup>35</sup> is lost.

Juvenile squid between 20 and 80 mm ML have been taken during all seasons in trawl surveys on the south coast at depths between 30 m and about 150 m. They are most abundant in autumn; at that time they are most numerous up to 50-m depth (Sauer and Augustyn, in prep.). Juveniles occur along most of the south coast in all seasons, but the highest densities are found from Cape St. Francis to Algoa Bay and to the east of Cape Agulhas. In spring there are very few small squid east of Algoa Bay and their abundance in the central region between 22° and 25°E is also very low. In autumn, abundance is high along the entire coast, with highest densities in the above-mentioned two areas and off Mossel Bay in the central area (Sauer and Augustyn, in prep.).

**Subadults and adults.** Maturation: The maturation process in squid has been investigated in several species, including *Loligo pealei*,<sup>36,37</sup> *L. opalescens*,<sup>38,39</sup> and *L. vulgaris reynaudii*.<sup>40</sup> In various studies of the last species, two maturity scales have been employed.<sup>13,14,16,40,41</sup>

From population studies by Augustyn<sup>13,14</sup> and Sauer,<sup>15</sup> it is known that size at maturity is highly variable and depends on the geographic location and time of the year. Males can be mature at 90 mm ML or immature at 250 mm ML, females at 100 and 180 mm ML, respectively.<sup>13</sup>

Predominantly mature squid occur on the spawning grounds throughout the year,<sup>14,15</sup> and a very high percentage of females there carry spermatophores in their buccal cavities.

Commercial catches have shown that mostly mature squid and occasional spent males occur on the spawning grounds. Smaller, immature squid are also present (Sauer and Augustyn, in prep.), but not in the immediate vicinity of the egg beds (W.H.H.S., diving observations).

Analysis of maturity data from the south coast has been examined by comparison of mean gonado-somatic index (GSI) values and the percentage of mature (stage 3) squid by area, depth range and season (Sauer and Augustyn, in prep.). In both males and females the GSI and the percentage of mature squid increases as one moves eastwards. In both sexes maturation rates are higher in the east than in the central or western areas, and maturation occurs at a smaller size in the spring than in autumn. These data support other evidence that squid spawn mainly in the east and are dispersed offshore and westward as they grow, and that maturation takes place as the population migrates back to the spawning grounds.

**Migration:** If the area from Plettenberg Bay to Algoa Bay up to 50-m depth contains the main spawning grounds, and little or no spawning occurs on the west coast, then it follows that some kind of migration cycle must be involved in transporting a large part of the biomass to the western and southern Agulhas Bank, where it is detected in SFRI biomass surveys. The scenario below postulates its probable occurrence, based on

seasonal length frequency, maturity, biomass and feeding data (Sauer and Augustyn, in prep.).

Squid paralarvae hatch mainly in spring and summer on the eastern spawning grounds, and their survival must depend largely on the dynamics of current systems and interactions with food sources (such as copepods) on and adjoining the main spawning grounds in the east (see trophic interactions, below).

If they survive the paralarval stage, they begin to swim more actively and their energy requirements increase. Juvenile squid eat larger crustaceans such as euphausiids and larval fish. Part of the juvenile population may migrate in a westerly direction in search of food as they increase in size, and tends to exploit food also at greater depths. By the time they have reached a size of around 100 mm ML, they feed almost exclusively on fish (see feeding, below) and they probably follow groups of prey species such as pelagic fish around the SW Agulhas Bank and up the west coast. Larger, but not generally fully mature squid, up to about 180 mm ML, may be found in deeper water down to about 200 m on the SW Agulhas Bank and down to over 300 m on the west coast.

Large, fully mature squid are most common at depths over 100 m on the shelf, and during peak spawning periods their abundance tends to increase towards the east, particularly on and in the vicinity of the spawning grounds.

As mentioned before, juveniles and subadults are found along the entire length of the south coast, despite the fact that most spawning takes place in the east. This suggests that a significant proportion of the population does not undertake a major migration westward, but grow and mature in the east, especially if food sources are abundant.

**Reproduction**

**Mating and spawning behaviour:** Squid pair off above the egg beds, and numerous pairs can be seen on any single occasion. Males outnumber females by about 2:1.<sup>14,15</sup> Copulation

(in the head-to-head and side-by-side positions) and spermatophore transfer have been observed. During the day females approach the egg mass with their arms in a cone formation, the males in close attendance just above and behind. The females then reach into the base of the egg bed to attach the egg capsules, sometimes disappearing almost entirely before re-emerging after a few seconds. Before deposition, the egg capsule is held in the arms of the female. Competition for females is often observed when lone males approach pairs and attempt to position themselves above the females. They are usually repulsed by the attendant male.

At night, pairing appears to break down, and females deposit egg capsules without an attendant male.<sup>42</sup> Chokka squid is probably an intermittent (serial) spawner,<sup>2,40</sup> but the duration of spawning by individuals is unknown.

**Location and timing of spawning:** Clusters of *L. v. reynaudii* egg capsules are common between Kleinbaai (to the east of Danger Point),<sup>13</sup> and East London in the east,<sup>14,15,21,42</sup> in about 5% of trawl nets at depths to 130 m between Mossel Bay and Port Elizabeth during offshore biomass surveys on the south coast (Roberts and Sauer, in prep.). Wallace *et al.*<sup>43</sup> reported eggs in about 20% of inshore trawl stations between Mossel Bay and Algoa Bay, with most occurring between Plettenberg Bay and Algoa Bay. The most westerly record is from Robben Island, near Cape Town. However, Augustyn<sup>14</sup> and Sauer *et al.*<sup>24</sup> concluded that the main spawning area was located between Plettenberg Bay and Algoa Bay. Some spawning sites are used repeatedly within a particular year and in subsequent years, suggesting that there are preferred conditions for spawning sites,<sup>24</sup> but there may be greater flexibility in spawning-site selection in this species than has been reported to date for other loliginids, such as *Photololigo edulis* and *L. opalescens*.<sup>44,45</sup>

Spawning also occurs in deep water, down to 130 m, mainly on the eastern Agulhas Bank (Fig. 7), but its extent, viability and contribution to recruitment have yet to be assessed.

While some spawning may occur year-round, there is some-

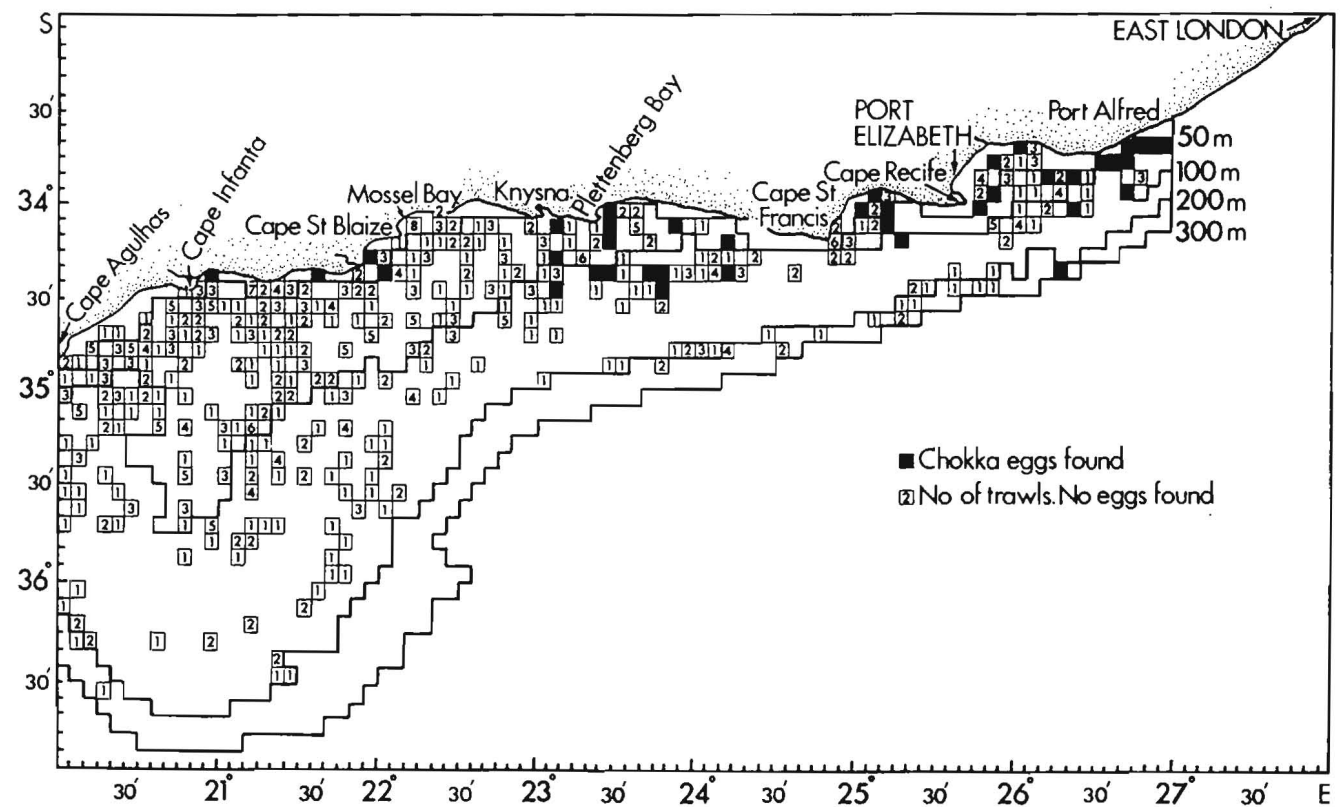


Fig. 7. The occurrence of chokka squid spawning as detected by eggs trawled during biomass surveys on the south coast 1985–1992. Figures in 5 × 5-nautical mile square blocks indicate the number of times each block was trawled; shaded squares indicate positive hauls of eggs.

times one, but generally two, peak periods, a major and a minor one, per annum. Although these may also be variable, they generally occur in spring and early summer (September to December) and in autumn or winter (March to July). These coincide with seasonal peaks of inshore catches (Fig. 8).

**Spawning substratum type:** Augustyn<sup>14</sup> reported eggs in the vicinity of low, shelving reefs interspersed with sand or reefs with occasional sand patches, usually of a coarse shell-grit. Sauer *et al.*<sup>24</sup> have subsequently found in a more comprehensive survey that fine sand or low-profile reef is the preferred substratum. Egg capsules are anchored by forming a cement-like blob of sand around the completely interwoven stalks, as in *L. pealei*.<sup>46</sup> It is possible that a specific grain size is most effective in forming a good anchorage, as suggested by Augustyn.<sup>14</sup>

**Schooling behaviour:** *L. vulgaris reynaudii* probably displays schooling behaviour as soon as it begins to swim. Squid aggregations on the shelf, which consist mainly of subadults, tend to spend the day feeding near the bottom.<sup>13,16</sup> There is also some evidence of sexual segregation in the subadult phase.<sup>16</sup> Trawl surveys have shown that squid are widely distributed over the entire shelf, and the pattern of catches supports the view that, during this phase, schools are numerous and much less dense than during the spawning phase. Sauer *et al.*<sup>24</sup> have found that squid migrate in discrete schools separated by sex in the vicinity of spawning sites and that mixing takes place during spawning. The latter have described the basic school types seen on the spawning grounds by correlating echo-sounder traces with diving observations (Fig. 9). They have also proposed a general classification of behaviour of schooling squid.

#### Age and growth

The question of squid longevity has not been clearly elucidated;<sup>47</sup> nevertheless, chokka age readings from statoliths show some promise (Fig. 10; see Lipiński<sup>48</sup>). There are indications that the largest chokka squid males (ML 400–450 mm) may live more than 15 months (Lipiński and Durholtz, in prep.). Validation experiments are needed to confirm these readings.

Results from Forsythe and Hanlon<sup>49</sup> indicate that, in *L. forbesi*, growth rates can be extremely variable, depending mainly on temperature, but possibly also on other factors such as food quality and availability. Extensive sampling on the population level may therefore be required to address variability (see Caddy<sup>50</sup> and Dawe and Natsukari<sup>51</sup>).

In the absence of an age database, analysis of length–frequency data by tracing the advancement of cohorts can be employed to provide guidelines for the understanding of size shifts over time, despite the reservations expressed by Caddy.<sup>50</sup>

There are usually three major cohorts present in the area of distribution at any time of the year. If it is assumed that the juvenile group has originated from the most recent spawning, and the subadult group from the previous one, then these two groups would be approximately six months apart. Therefore, the currently spawning large, mature group is likely to be about 18 months old. This means that there may be two overlapping generations (see, for example, Mesnil<sup>52</sup> and Sauer<sup>14</sup>), but this awaits confirmation from statolith-based ageing studies.

This scenario is complicated by the fact that the major mating and spawning periods may extend over several months, that their timing is variable, that attainment of maturity is also variable and that schools are segregated by sex (and to some extent size).<sup>24</sup> Some squid born early in a given spawning period may mature early enough to mate and spawn by the end of the next spawning period, that is, at between 14 and 17 months, while others may mature too late and then spawn early in the next spawning period, i.e. at between 20 and 23 months.

#### Post-spawning mortality

There has been much speculation (e.g. Augustyn<sup>13</sup>) about the occurrence of post-spawning mortality, a feature of the life cycle known at least for some species of cephalopods. *L. opalescens*, for example, deteriorate rapidly during and after spawning<sup>45</sup> and die in vast numbers on the spawning grounds,<sup>23</sup> but this has not been found in *L. vulgaris reynaudii*.<sup>21,24,42</sup> In contrast, dispersal after spawning and before death may be more prevalent in chokka squid. Weak and dying individuals could be highly susceptible to predation and cannibalism, and this could contribute to the disappearance of squid soon after spawning.

Despite uncertainty about its longevity and the variability found in many aspects of its biology and ecology, many features of the life cycle of *L. vulgaris reynaudii* appear to be similar to those of several other loliginids, notably *L. vulgaris vulgaris*, *L. pealei* and to a lesser extent *L. opalescens*, the life cycles of which have been summarized in Boyle.<sup>53</sup> They develop quickly, before hatching as fully developed juveniles, have high metabolic and growth rates, undertake feeding and spawning migrations, play an important trophic role as both predators and prey, and generally spawn in environments where food for their paralarvae is likely to be abundant. They also appear to be subject to post-spawning mortality, though this has not yet been documented for chokka squid.

#### Ecology

##### Trophic interactions

**Feeding and survival of paralarvae:** Augustyn *et al.*<sup>1</sup> highlighted the critical phase after hatching when paralarvae must find suitable food within a few days to survive, and speculated

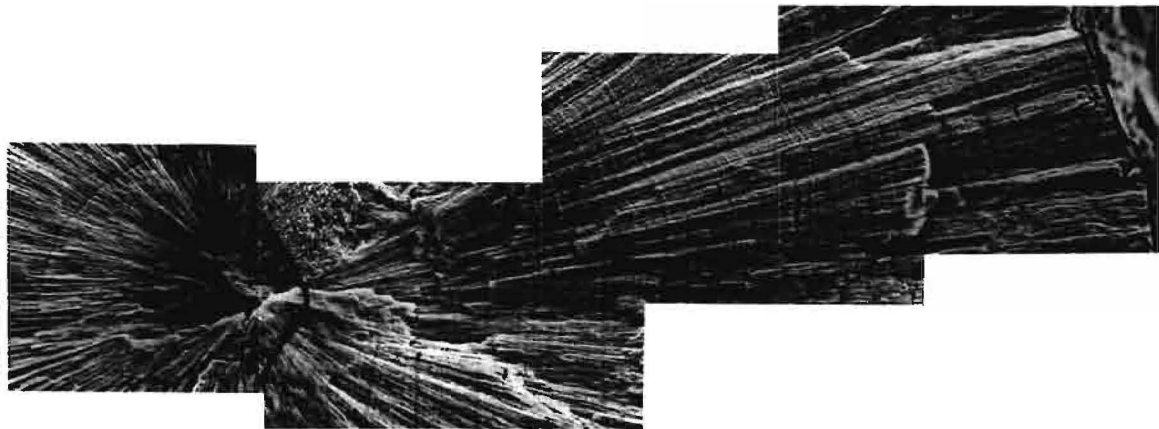


Fig. 8. Chokka squid statolith broken in the frontal plane and etched with 1% HCl. Juvenile male, 36 mm ML. Number of increments about 190.

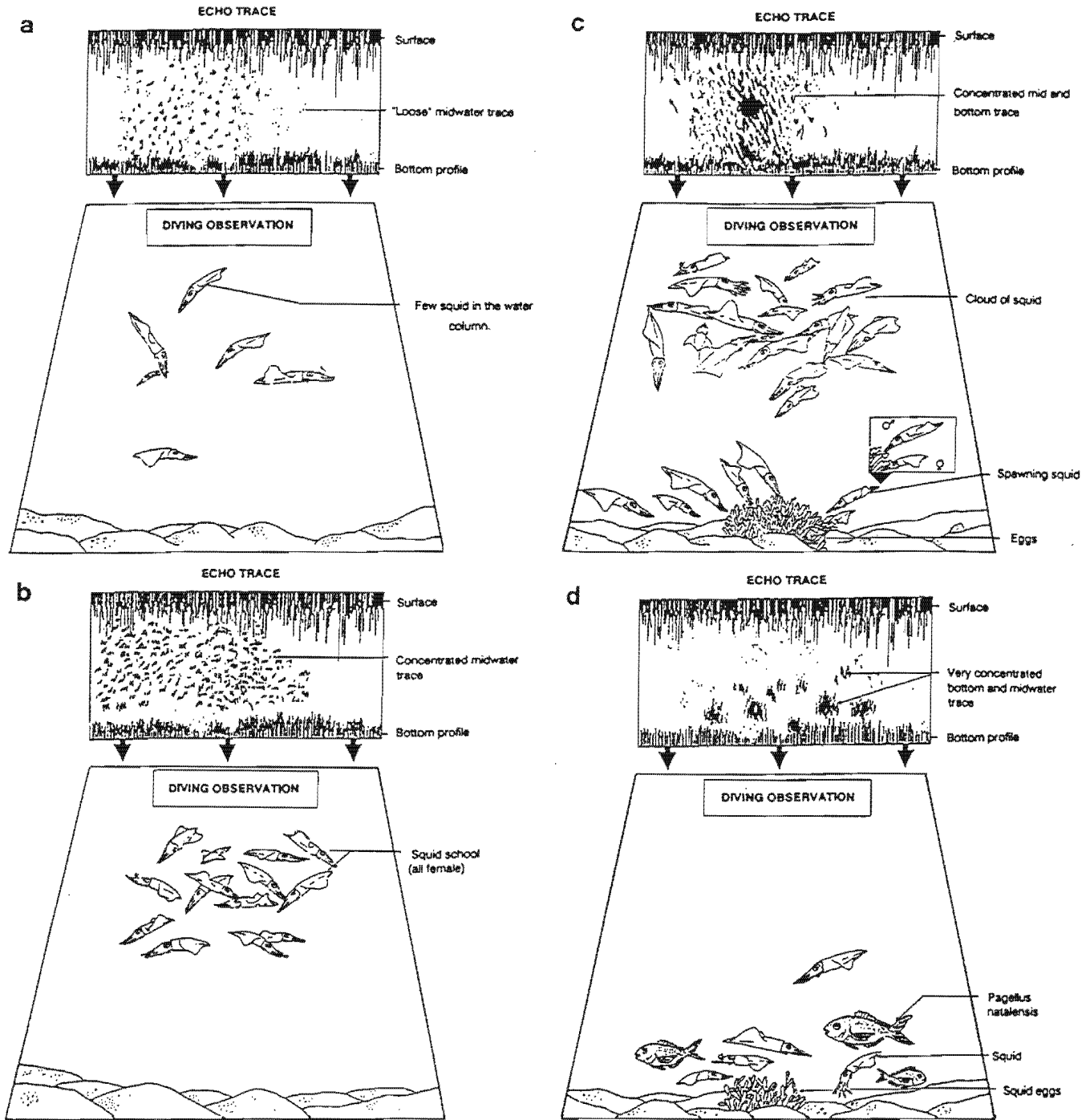


Fig. 9. Comparison of echo-traces and diving observations made on spawning sites. a, Loose patches; b, dense patches; c, complex pattern; d, strong echo-traces of fish with few squid (from Fig. 8, Sauer *et al.*<sup>24</sup>).

on their interaction with plankton concentrations. There is no direct evidence for the identity of their prey because the paralarvae frequently do not ingest hard parts of their prey.<sup>1</sup> The copepod *Calanus agulhensis* is, however, taken in the laboratory (C.J.A., pers. obs.). This is the dominant copepod on the Agulhas Bank, comprising 44–64% of the total copepod biomass on the western Bank and 57–85% on the eastern Bank,<sup>54</sup> and is likely to be the main prey species for paralarvae. The centre of abundance of this species, together with that of its developmental stages, lies to the south of Mossel Bay in the vicinity of the 'cool upwelling ridge', mid-shelf of the eastern/central Bank<sup>55</sup> (Fig. 11, Largier *et al.*<sup>56</sup>). Boyd *et al.*<sup>57</sup> have suggested that there is cyclonic circulation associated with the ridge, accounting for the retention of *Calanus* life-history stages within this region, although a small net westward move-

ment is evident from distribution patterns.<sup>55,56</sup> Such a gyral circulation is also of significance for squid paralarvae, ensuring that they are retained within the eastern/central Agulhas Bank where plankton food is abundant, and not advected westwards where food is less abundant.

**Feeding:** Only late juveniles (generally larger than 60 mm ML) or adults have been investigated, and results indicate that food types, feeding indices and feeding times are subject to great variability which is very inadequately understood<sup>9,58</sup> (also Lipiński in prep.). Chokka squid are opportunistic predators,<sup>9</sup> taking prey with a wide size range throughout the water column over their entire geographical range.

Non-spawning squid investigated in St. Francis Bay, smaller than 126 mm ML, fed mostly on crustaceans and on fish when larger.<sup>59</sup> This shift in diet was investigated on the south coast<sup>12</sup>



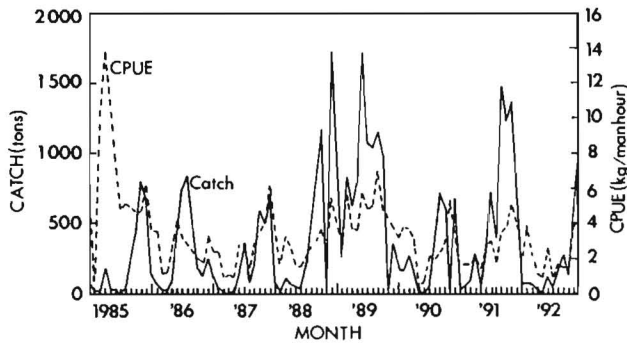


Fig. 10. Monthly catch and catch per unit effort (CPUE) trends in the chokka squid jig fishery.

and is likely to be similar on the west coast<sup>16</sup> because most large, schooling squid species follow the same pattern.<sup>60</sup> In loliginid squid, the diet also tends to broaden with increasing size.<sup>59,61</sup>

Cannibalism is generally low offshore<sup>13</sup> (also Lipiński in prep.), but it increases on the spawning grounds, especially during the day.<sup>58</sup>

On the feeding grounds (which include most of the offshore shelf of the south and west coast), subadult squid feed on or near the bottom during the day and tend to follow their prey into the upper layers at night. They may feed at any time of the 24-hour cycle but generally feeding is more intense at night<sup>59</sup> (also Lipiński in prep.). The diet varies seasonally; on the west coast more crustaceans are eaten in winter than in summer, but less fish.<sup>16</sup> This trend is not so pronounced on the south coast (Lipiński in prep.). Eating fish gives the adult squid an energetic advantage, as crustaceans eaten are smaller than fish and digested more slowly.<sup>62,63</sup> Among crustaceans they eat mainly euphausiids, amphipods and megalopae larvae; among fish, various non-commercial fish larvae and juveniles, dragonettes, anchovy and hake.<sup>9,13,16,59</sup> It is estimated that anchovy forms approximately one-third of the chokka's fish diet by mass on the feeding grounds. This is, however, subject to considerable variation<sup>9</sup> (Lipiński in prep.).

When squid migrate to the spawning grounds, their feeding and diet change markedly. Food composition and consumption on the spawning grounds was examined by Augustyn<sup>14</sup> and Sauer and Lipiński.<sup>58</sup>

Predation: Several studies of squid predators have revealed that *L. vulgaris reynaudii* is prey to numerous species,<sup>2,64-72</sup> but details of interactions are poorly understood. Some of these interactions are discussed by Lipiński.<sup>9</sup> Augustyn<sup>13</sup> compiled a list of known predators of chokka from published works (up to 1988).

Predation on paralarvae has not been investigated. Published information on predation on juveniles exists for only two species of fish: *Zeus faber* and *Lepidopus caudatus*.<sup>67</sup> Young squid (mean size 150 mm ML) is taken by the fur seal *Arctocephalus pusillus pusillus*.<sup>71</sup> Mainly large juveniles or adults of a wide size range are taken by large fish predators: kob *Argyrosomus hololepidotus*,<sup>66</sup> santer *Cheimerius nufar*,<sup>64</sup> elf *Pomatomus saltatrix* and albacore *Seriola lalandii*,<sup>65,69</sup> hake *Merluccius capensis* and monk *Lophius vomerinus*.<sup>72</sup> Chokka squid are an important food of various elasmobranchs.<sup>69,73</sup>

Some seabird species may take squid, depending on the availability of other food, such as Cape gannets *Morus capensis*<sup>74,75</sup> and penguins *Spheniscus demersus*,<sup>76</sup> but procellariiform seabirds (surface-feeding on dead squid) consume only small amounts.<sup>70,77</sup>

The quantification of predation on an annual scale is very difficult, because most of these predators are highly opportunistic.<sup>9</sup> Even general descriptions of concepts about predation on

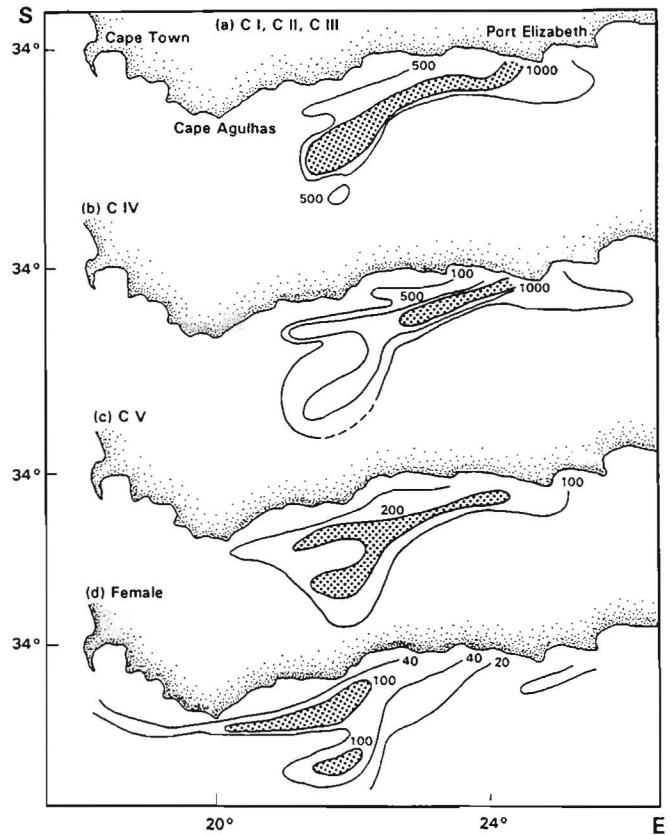


Fig. 11. The distribution of successive developmental stages (as number per m<sup>3</sup>) of the dominant copepod, *Calanus agulhensis*, on the Agulhas Bank in November 1999. a, Copepodite stages I, II and III; b, copepodite stage IV; c, copepodite stage V; d, females (after Largier *et al.*,<sup>56</sup> with permission.)

squid are very preliminary and unsatisfactory, due to the selective and irregular nature of sampling, poor knowledge of their feeding behaviour, and small sample sizes.<sup>78</sup>

Surprisingly few predators have been recorded on the spawning grounds, though fishing, diving and observations from remotely operated vehicles have been employed regularly.<sup>21,42,69</sup> Squid found in stomachs of predators were not spent.<sup>69</sup> Only one species of teleost and one elasmobranch was found to have ingested squid eggs.

#### Distribution and ecology related to the environment

Reviews of the oceanography of the Agulhas Bank have been produced by Boyd and Shillington,<sup>79</sup> Boyd *et al.*<sup>57</sup> and Largier *et al.*<sup>56</sup> Relatively little knowledge exists about the influence of this environment on chokka squid.

Initial environmental work was restricted to direct statistical approaches such as correlation and regression analyses between environmental factors and catches. The first work of this nature was undertaken in False Bay by Augustyn,<sup>13</sup> factors such as wind speed and direction, time of day, lunar phase, surface temperature, and their effect on jigged catch rates were considered. Temperature had the greatest influence, with the best mean catches taken above 17°C. In another study on the west coast, results indicated that both bottom temperature and oxygen levels were influential, with the 8°C isotherm and 3.5 ml l<sup>-1</sup> O<sub>2</sub> apparently limiting the distribution of adult chokka squid.<sup>16</sup> Time of day was shown to be an important factor, because squid migrate vertically in the water column after dark. Later, Sauer *et al.*<sup>80</sup> showed a statistical correlation between nearshore temperatures along the eastern Cape coast and jigged inshore catch rates, with enhanced catches during temperature drops induced by coastal upwelling.

More recently, there has been a greater emphasis on research into the interaction between squid and the environment, as a result of resource management needs. Roberts (in prep.), using a very large data set, investigated the potential influence of ocean temperature on the distribution and abundance of chokka squid. He showed that a direct correlation was not obvious and that squid were adapted to a wide temperature range (between 8°C and 22°C). Able to cope with rapid temperature changes, they can easily move through the thermocline. Temperature is therefore probably not a primary factor affecting distribution, but rather food availability.

The greatest potential for the influence of the physical environment arises during the spawning, egg incubation and larval phases of the squid life cycle. Consequently, this has become a focal point for much of the environmental research presently under way.

It was earlier assumed<sup>14</sup> that the spawning areas acted as protected sanctuaries and that environmental conditions there must be favourable for spawning; for example, the sandy substratum of the bays allows good anchoring for egg clusters, oxygen levels are always high and wave activity ensures eggs were well aerated; also that warm water temperatures prevailed in summer and were conducive to optimal egg incubation. This was supported by an experiment which indicated that water temperatures between 12° and 20°C are optimal for hatching.<sup>13</sup>

Recent research on the oceanography of the Agulhas Bank shelf and adjacent inshore waters, the spawning habitat of chokka squid, and egg development, hatching and survival rates, suggests that this scenario is an oversimplification and calls for a revision of these initial hypotheses (Roberts, in prep.). The inshore region of the eastern Cape is not the protected sanctuary previously believed. It is, on the contrary, a region of great environmental variability. Because of coastal upwelling, sea temperatures vary greatly, particularly in early summer during the peak spawning season, and eggs are commonly exposed to rapid and extreme changes of as much as from 24° to 9°C.

Preliminary data also suggest that wave activity near the seabed stirs up sediment in the inshore region, which not only causes the adult spawners to avoid these areas at times but also has the potential to bury egg beds resulting in egg mortality (Roberts, in prep.).

Chokka squid also spawn to a large extent in much deeper shelf waters than was previously thought, greater than 100 m (see Fig. 7). At these depths, light levels, wave activity (aeration) and bottom temperatures are relatively low (Roberts, in prep.). The implication is that spawning may generally occur in the embayments, but the squid may move or remain offshore to spawn if conditions are not favourable inshore.

Sea conditions may have an equally important influence on paralarvae. It is not yet known whether or not hatchlings are able to migrate vertically through the water column to access planktonic food in the upper mixed layer. Their ability to do so also has important implications for their dispersion because near-surface currents on the inner shelf, being primarily wind-driven, are generally faster than deeper-moving ones<sup>81</sup> (see also Roberts and Goschen, in prep.).

An investigation into long-term and large-scale environmental effects on chokka squid (Roberts, in prep.) has revealed two instances where it would appear that the environment has had a major impact on the squid fishery. The first event occurred during 1988/89 when catches (Fig. 12) greatly increased. This was apparently related to an inshore cold-water anomaly off the south coast which, it is postulated, could have been induced by the Agulhas Current. The second event relates to the poor jig catches in 1992. One of the probable effects of

the El Niño event in 1992 was an intensification of atmospheric conditions in winter, when winds caused an increase in the wave field over the south coast, in terms of wave height, period and frequency. Observations and preliminary turbidity data also showed that the increased wave field had the effect of stirring up the inshore sea-bed on the inshore spawning grounds, causing the adults to avoid these areas to a greater extent than usual, and consequently not being available to the jig fishery.

## Conclusions

How can knowledge of the life history and ecology of chokka squid be of benefit to the squid fishery and to those involved with rational management of the stock?

As far as the fishery and stock management are concerned, problems revolve around the variability in size and its availability to fisheries. Planning would be facilitated if research enabled predictions to be made of the size of stock from recruitment, on the timing of spawning aggregations, and on the most productive areas.

On predicting stock size from recruitment: Stock size and recruitment of juveniles on the shelf can now be monitored, and the acoustic methodology, once fully developed, may well enable spawning stock size to be measured. To be able to predict changes in stock size in advance, however, and to develop models of stock behaviour for assessment and management purposes, it is essential to determine the nature of the stock-recruitment relationship. Measuring recruitment implies being able to establish an egg, paralarval or juvenile abundance index with some confidence. There is at present no reliable annual time series for any of these, but in the case of juveniles, a longer time series of biomass surveys may indicate whether such a relationship exists. Estimating paralarval abundance involves far more daunting problems, because this may require widespread and intensive sampling, and an understanding of

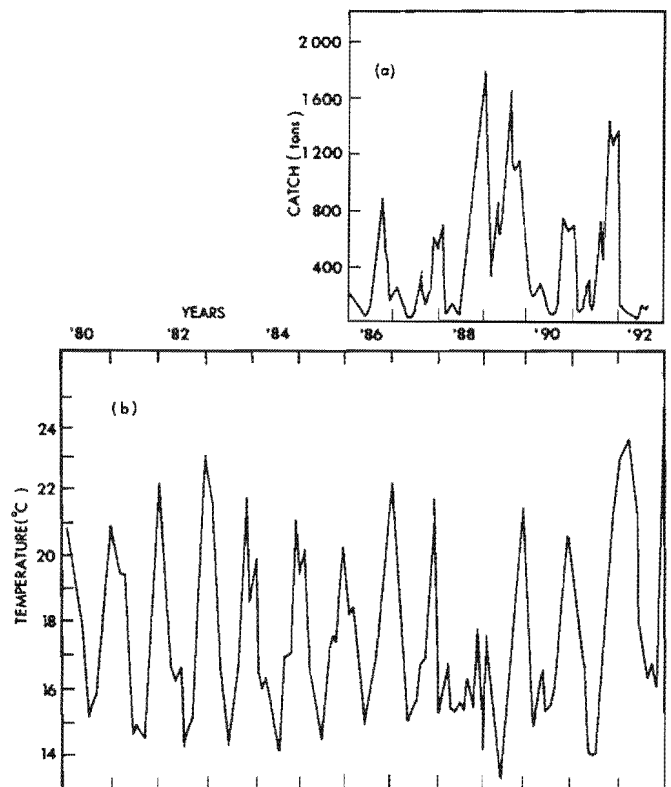


Fig. 12. a, Squid catch time series, showing large catches in 1988/89. b, Cold water anomaly in coastal waters off Knysna, which coincided with large squid catches.

paralarval predator-prey dynamics. In this regard, understanding paralarval-copepod interactions is of paramount importance, because food availability is critical to paralarval survival and therefore to recruitment of the next cohort. The quantitative dynamics of paralarval distribution in relation to copepod distribution is the key aspect here. We are still in the early stages of this research: data on the seasonal distribution and abundance of paralarvae and copepods are being collected and analysed. Determining egg abundance may be a useful initial guide to recruitment and subsequent abundance of spawning stock. In the case of the latter, determination of the average fecundity of females is essential.<sup>22</sup>

On abundance and availability to the fishery: to understand the timing of spawning aggregations and the factors influencing productivity in certain areas, the inshore environment and its variability must be better understood. The first analyses of data from the environmental monitoring stations indicate that there may be links between temperature and weather conditions (such as swell and turbidity) and the availability of squid on the grounds.

On management of the squid resource: the effects and effectiveness of control measures such as closed seasons and closed areas, and assessment of the effects of heavy fishing pressure and fishing methods (e.g. use of lights, anchors and anchor chains) on spawning aggregations directly relate to the fishery and its management. This fishery is based almost entirely on spawning concentrations and the danger of adversely affecting recruitment would be considerable without control measures. Biological studies on the spawning grounds have confirmed that the most effective period for closures is in October/November, and initial results of studies in the Tsitsikamma Coastal National Park closed area indicate that it is an important spawning area, with squid moving across the Park boundaries. Long-term research needs to address whether fishing adversely affects spawning behaviour.

These are a few examples of how biological and oceanographic studies related to the squid's life cycle could directly assist management.

Authors' note: Some readers may be critical of the large number of research reports quoted as in preparation. We wish to point out that much of the work mentioned in this paper is still in progress under the auspices of the Sea Fisheries Research Institute's Squid Working Group. Further information on these matters may be sought from the Convener, Squid Working Group, SFRI, Private Bag X2, Rogge Bay, 8012 South Africa.

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1. Augustyn C.J., Lipiński M.R. and Sauer W.H.H. (1992). Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. In *Benguela Trophic Functioning*, eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* 12, 903-918.
2. Sauer W.H.H. (1993). *The ecology of spawning squid Loligo vulgaris reynaudii in the inshore waters of the eastern Cape*. Ph.D. thesis, University of Port Elizabeth.
3. Caddy J.F. (1983). The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. In *Advances in Assessment of World Cephalopod Resources*, ed. J.F. Caddy. *FAO Fish. Tech. Pap.* 231, 416-452.
4. O'Dor R.K. (1992). Big squid in big currents. In *Benguela Trophic Functioning*, eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* 12, 225-235.
5. Murata M. (1989). Population assessment, management and fishery forecasting for the Japanese common squid, *Todarodes pacificus*. In *Marine*

*Invertebrate Fisheries: Their Assessment and Management*, ed. J.F. Caddy, pp. 613-636. Wiley, New York.

6. Squires H.J. (1957). Squid, *Illex illecebrosus* (Lesueur), in the Newfoundland fishing area. *J. Fish. Res. Board Can.* 14, 693-728.
7. Recksiek C.W. and Frey H.W. (eds.) (1978). Biological, oceanographic and acoustic aspects of the market squid, *Loligo opalescens* Berry. *Fish Bull., Calif.* 169, 1-185.
8. Natsukari Y. and Tashiro M. (1991). Neritic squid resources and cuttlefish resources in Japan. *Mar. Behav. Physiol.* 18, 149-226.
9. Lipiński M.R. (1992). Cephalopods and the Benguela ecosystem: trophic relationships and impact. In *Benguela Trophic Functioning*, eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* 12, 791-802.
10. Hatanaka H., Sato T., Augustyn C.[J.], Payne A.[I.L.] and Leslie R.[W.] (1983). Report on the Japan/South Africa joint trawling survey on the Agulhas Bank in November/December 1980. *Spec. Publ. mar. Fish. Resour. Cent.*, 1-73.
11. Uozumi Y., Hatanaka H., Payne A.[I.L.] and Augustyn [C.]J. (1985). Report on the Japan/South Africa joint trawl survey of groundfish resources on the Agulhas Bank in June 1982. *Publ. Far Seas Fish. Res. Lab., S Series* 13, 1-78.
12. Uozumi Y., Hatanaka H., Sato T., Augustyn [C.]J., Payne A.[I.L.] and R.[W.] Leslie (1984). Report on the Japan/South Africa joint trawling survey on the Agulhas Bank in November/December 1981. *Publ. Far Seas Fish. Res. Lab., S Series* 11, 1-91.
13. Augustyn C.J. (1989). *Systematics, life cycle and resource potential of the chokker squid Loligo vulgaris reynaudii*. Ph.D. thesis, University of Port Elizabeth.
14. Augustyn C.J. (1990). Biological studies on the chokker squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) on spawning grounds off the south-east coast of South Africa. *S. Afr. J. mar. Sci.* 9, 11-26.
15. Sauer W.H.H. (1991). *Population characteristics of the chokker squid, Loligo vulgaris reynaudii, and its distribution in the Algoa Bay-St Francis Bay area in relation to environmental conditions*. M.Sc. thesis, University of Port Elizabeth.
16. Augustyn C.J. (1991). The biomass and ecology of chokka squid *Loligo vulgaris reynaudii* off the west coast of South Africa. *S. Afr. J. Zool.* 26, 164-181.
17. Augustyn C.J. (1986). The squid jigging fishery on the South Africa south coast. *S. Afr. Shipp. News Fishg Ind. Rev.* 41 (5), 24, 26.
18. Augustyn C.J. and Grant W.S. (1988). Biochemical and morphological systematics of *Loligo vulgaris vulgaris* Lamarck and *Loligo vulgaris reynaudii* D'Orbigny nov. comb. (Cephalopoda: Myopsida). *Malacologia* 29 (1), 215-233.
19. Hampton I. (1987). Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. In *The Benguela and Comparable Ecosystems*, eds. A.I.L. Payne, J.A. Gulland and K.H. Brink. *S. Afr. J. mar. Sci.* 5, 557-564.
20. Jefferts K., Burczynski J. and Percy W.G. (1987). Acoustical assessment of squid (*Loligo opalescens*) off the Oregon coast. *Can. J. Fish. aquat. Sci.* 44, 1261-1267.
21. Augustyn C.J., Roel B.A. and Cochrane K.L. (1993). Stock assessment in the chokka squid *Loligo vulgaris reynaudii* fishery off the coast of South Africa. In *Recent Advances in Cephalopod Fisheries Biology*, eds. T. Okutani, H. Hatanaka and R.K. O'Dor, pp. 3-14. Tokai University Press, Tokyo.
22. Sauer W.H.H., McCarthy C., Smale M.J. and Koorts A.S. (in press). A detailed examination of chokka squid (*Loligo vulgaris reynaudii*) spawning grounds in the Kromme Bay, South Africa. *Bull. mar. Sci.*
23. Fields W.G. (1965). The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. *Fish Bull. Dep. Fish Game (USA)* 131, 1-108.
24. Sauer W.H.H., Smale M.J. and Lipiński M.R. (1992). The location of spawning grounds, spawning and shoaling behaviour of the squid *Loligo vulgaris reynaudii* (D'Orbigny) off the eastern Cape coast, South Africa. *Mar. Biol.* 114, 97-107.
25. Naef A. (1928). Die Cephalopoden (Embryologie). Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Friedlander und Sohn, Berlin. *Monographia* 35 (2), 1-357.
26. Von Boletzky S. (1987). Embryonic phase. In *Cephalopod Life Cycles Vol. 2, Comparative Reviews*, ed. P.R. Boyle, pp. 5-31. Academic Press, London.
27. Von Boletzky S. (1989). Recent studies on spawning, embryonic development, and hatching in the Cephalopoda. *Adv. mar. Biol.* 25, 85-115.
28. Mangold-Wirz K. (1963). Biologie des céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie Milieu Suppl.* 13, 1-285.
29. Worms J. (1983). *Loligo vulgaris*. In *Cephalopod Life Cycles. 1. Species Accounts*, ed. P.R. Boyle, pp. 143-157. Academic Press, London.
30. Arnold J.M. (1965). Normal embryonic stages of the squid *Loligo pealii* (LeSueur). *Biol. Bull. mar. biol. Lab., Woods Hole* 128, 24-32.

31. Young R.E. and Harman R.F. (1989). 'Larva', 'paralarva' and 'subadult' in cephalopod terminology. *Malacologia* 29 (1), 201-207.
32. Trites R.W. (1983). Physical oceanographic features and processes relevant to *Illex illecebrosus* spawning in the western North Atlantic and subsequent larval distribution. *NAFO Sci. Coun. Studies* 6, 39-55.
33. Rowell T.W., Trites R.W. and Dawe E.G. (1985). Distribution of short-finned squid (*Illex illecebrosus*) larvae and juveniles in relation to the Gulf Stream frontal zone between Florida and Cape Hatteras. *NATO Sci. Coun. Studies* 9, 77-92.
34. Arkhipkin A.I. and Fedulov P.P. (1986). Diel movements of juvenile *Illex illecebrosus* and other cephalopods in the shelf water-slope water frontal zone off the Scotian shelf in spring. *J. NW. Atl. Fish. Sci.* 7, 15-24.
35. McConathy D.A., Hanlon R.T. and Hixon R.F. (1980). Chromatophore arrangements of hatching loliginid squids (Cephalopoda, Myopsida). *Malacologia* 19, 279-288.
36. Vovk A.N. (1972). Method of determining maturing stages in gonads of the squid *Loligo pealei*. *Zoologicheskii Zh.* 51, 127-132 (in Russian).
37. Selman K. and Arnold J.M. (1977). On ultrastructural and cytochemical analysis of oogenesis in the squid, *Loligo pealei*. *J. Morph.* 152, 381-400.
38. Grieb T.M. and Beeman R.D. (1978). A study of spermatogenesis in the spawning population of the squid, *Loligo opalescens*. *Fish Bull. Calif. Dep. Fish Game (USA)* 169, 11-22.
39. Knipe J.H. and Beeman R.D. (1978). Histological observations on oogenesis in *Loligo opalescens*. *Fish Bull. Calif. Dept. Fish Game (USA)* 169, 23-34.
40. Sauer W.H.H. and M.R. Lipiński (1990). Histological validation of morphological stages of sexual maturity in chokker squid *Loligo vulgaris reynaudii* D'Orb. (Cephalopoda: Loliginidae). *S. Afr. J. mar. Sci.* 9, 189-200.
41. Lipiński M.R. (1979). Universal maturity scale for the commercially-important squids (Cephalopoda: Teuthoidea). The results of maturity classifications of the *Illex illecebrosus* (Lacépède, 1821) populations for the years 1973-1977. *Res. Doc. int. Comm. NW. Atl. Fish.* 79/11/38, 1-40.
42. Sauer W.H.H. and Smale M.J. (1993). Spawning behaviour of *Loligo vulgaris reynaudii* in shallow waters of the south-eastern Cape, South Africa. *Symp. In Recent Advances in Cephalopod Fisheries Biology*, eds. T. Okutani, H. Hatanaka and R.K. O'Dor, pp. 489-498. Tokai University Press, Tokyo.
43. Wallace J.H., Kok H.M., Buxton C.D. and Bennett B.A. (1984). Inshore small-mesh trawling survey of the Cape south coast. 1. Introduction, methods, stations and catches. *S. Afr. J. Zool.* 19, 154-164.
44. Natsukari Y. (1978). Scuba diving observations on the spawning ground of the squid, *Doryteuthis kensaki* (Wakiya et Ishikawa, 1921) (Cephalopoda, Loliginidae). *Venus, Kyoto* 45 (4), 206-208.
45. Hixon R.F. (1983). *Loligo opalescens*. In *Cephalopod Life Cycles. I. Species Accounts*, ed. P.R. Boyle, pp. 95-114. Academic Press, London.
46. Arnold J.M. (1962). Mating behavior and social structure in *Loligo pealii*. *Biol. Bull. mar. biol. Lab., Woods Hole* 123, 53-57.
47. Jereb P., Ragonese S. and von Boletzky S. (eds.) (1991). *Squid Age Determination Using Statoliths*. N.T.R.-I.T.P.P. Special Publication no 1, Mazara del Vallo, Italy.
48. Lipiński M.R. (1991). A laboratory manual. Scanning electron microscopy (SEM) and chemical treatment. In *Squid Age Determination Using Statoliths*, eds. P. Jereb, S. Ragonese and S. von Boletzky, pp. 97-112. N.T.R.-I.T.P.P. Special publication no 1, Mazara del Vallo, Italy.
49. Forsythe J.W. and R.T. Hanlon (1989). Growth of the eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda). *Aquacult. Fish. Mgmt* 20, 1-14.
50. Caddy J.F. (1991). Daily rings on squid statoliths: an opportunity to test standard population models? In *Squid Age Determination Using Statoliths*, eds. P. Jereb, S. Ragonese and S. von Boletzky, pp. 53-66. N.T.R.-I.T.P.P. Special Publication no 1, Mazara del Vallo, Italy.
51. Dawe E.G. and Y. Natsukari (1991). Practical procedures of squid ageing using statoliths. A laboratory manual. Light microscopy. In *Squid Age Determination Using Statoliths*, eds. P. Jereb, S. Ragonese and S. von Boletzky, pp. 83-95. N.T.R.-I.T.P.P. Special Publication no 1, Mazara del Vallo, Italy.
52. Mesnil B. (1977). Growth and life cycle of squid, *Loligo pealei* and *Illex illecebrosus*, from the Northwest Atlantic. *ICNAF Sel. Papers* 2, 55-69.
53. Boyle P.R. (ed.) (1983). *Cephalopod Life Cycles. I. Species Accounts*. Academic Press, New York.
54. Verheyne H.M., Huggett J.A., Hutchings L., Painting S.J. and Peterson W.T. (1994). The dynamics of the Agulhas Bank ecosystem: a synthesis of existing knowledge of the functioning of the Agulhas Bank ecosystem and its implications for resource production and variability: zooplankton food chains: microheterotrophs or mesozooplankton? *S. Afr. J. Sci.* 90, 154-165.
55. Peterson W.T., Hutchings L., Huggett J.A. and Largier J.C. (1992). Anchovy spawning in relation to the biomass and the replenishment rate of their copepod prey on the western Agulhas Bank. In *Benguela Trophic Functioning*, eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* 12, 487-500.
56. Largier J.L., Chapman P., Peterson W.T. and Swart V.P. (1992). The western Agulhas Bank: circulation, stratification and ecology. In *Benguela Trophic Functioning*, eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* 12, 319-339.
57. Boyd A., Taunton-Clark J. and Oberholster G.P.J. (1992). Spatial features of the near-surface and midwater circulation patterns off western and southern South Africa and their role in the life histories of various commercially fished species. In *Benguela Trophic Functioning*, eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* 12, 189-206.
58. Sauer W.H.H. and Lipiński M.R. (1991). Food of squid *Loligo vulgaris reynaudii* D'Orb. (Cephalopoda: Loliginidae) on their spawning grounds in eastern Cape, South Africa. *S. Afr. J. mar. Sci.* 10, 193-201.
59. Lipiński M.R. (1987). Food and feeding of *Loligo vulgaris reynaudii* from St Francis Bay, South Africa. In *The Benguela and Comparable Ecosystems*, eds. A.I.L. Payne, J.A. Gulland and K.H. Brink. *S. Afr. J. mar. Sci.* 5, 557-564.
60. Nixon M. (1987). Cephalopod diets. In *Cephalopod Life Cycles, 2, Comparative Reviews*, ed. P.R. Boyle, pp. 201-219. Academic Press, London.
61. LaRoe E.T. (1971). The culture and maintenance of the loliginid squids *Sepioteuthis sepioides* and *Doryteuthis plei*. *Mar. Biol.* 9, 9-25.
62. Lipiński M.R. (1990). Changes in pH in the caecum of *Loligo vulgaris reynaudii* during digestion. *S. Afr. J. mar. Sci.* 9, 43-51.
63. Hirtle R.W.M., De Mont M.E. and O'Dor R.K. (1981). Feeding, growth and metabolic rate in captive short-finned squid, *Illex illecebrosus*, in relation to the natural population. *J. Shellfish Res.* 1, 187-192.
64. Smale M.J. (1986). The feeding biology of four predatory reef fishes off the south-eastern Cape coast, South Africa. *S. Afr. J. Zool.* 21, 111-130.
65. Smale M.J. (1986). The feeding habits of six pelagic and predatory teleosts in eastern Cape coastal waters (South Africa). *J. Zool. Lond., Ser. B* 1, 357-409.
66. Smale M.J. and Bruton M.N. (1985). Predation and prey selectivity by *Argyrosomus hololepidotus* (Osteichthyes: Sciaenidae) in south-eastern Cape waters of South Africa. *S. Afr. J. Zool.* 20, 97-108.
67. Meyer M. and Smale M.J. (1991). Predation patterns of demersal teleosts from the Cape south and west coasts of South Africa. 1. Pelagic predators. *S. Afr. J. mar. Sci.* 10, 173-191.
68. Meyer M. and Smale M.J. (1991). Predation patterns of demersal teleosts from the Cape south and west coasts of South Africa. 2. Benthic and epibenthic predators. *S. Afr. J. mar. Sci.* 11, 409-422.
69. Sauer W.H.H. and Smale M.J. (1991). Predation patterns on the inshore spawning grounds of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) off the eastern Cape, South Africa. *S. Afr. J. mar. Sci.* 11, 513-523.
70. Lipiński M.R. and Jackson S. (1989). Surface-feeding on cephalopods on procellariiform seabirds in the southern Benguela region, South Africa. *J. Zool., Lond.* 218, 549-563.
71. Lipiński M.R. and David J.H.M. (1990). Cephalopods in the diet of the South African fur seal (*Arctocephalus pusillus pusillus*). *J. Zool., Lond.* 221 (3), 359-374.
72. Lipiński M.R., Payne A.I.L. and Rose B. (1992). The importance of cephalopods as prey for hake and other groundfish in South African waters. In *Benguela Trophic Functioning*, eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* 12, 651-662.
73. Smale M.J. (1991). Occurrence and feeding of three shark species, *Carcharias brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the eastern Cape coast of South Africa. *S. Afr. J. mar. Sci.* 11, 31-42.
74. Klages N.T.W., Willis A.B. and Ross G.J.B. (1992). Variability in the diet of the Cape gannet at Bird Island, Algoa Bay, South Africa. In *Benguela Trophic Functioning*, eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* 12, 761-771.
75. Batchelor A.L. and Ross G.J.B. (1984). The diet and implications of dietary change of Cape gannets on Bird Island, Algoa Bay. *Ostrich* 55, 45-63.
76. Randall R.M., Randall B.M. and Klingelhoeffer E.W. (1981). Species diversity and size ranges of cephalopods in the diet of jackass penguins from Algoa Bay, South Africa. *S. Afr. J. Zool.* 16, 163-166.
77. Berruti A., Adams N.J. and Jackson S. (1989). *The Benguela ecosystem. Part VI. Seabirds. Oceanogr. mar. Biol. A. Rev.* 27, 273-335.
78. Punt A.E., Leslie R.W. and du Plessis S.E. (1992). Estimation of the annual consumption of food by Cape hake *Merluccius capensis* and *M. paradoxus* off the South African west coast. In *Benguela Trophic Functioning*, eds. A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* 12, 611-634.
79. Boyd A.J. and Shillington F.A. (1994). Physical forcing and circulation patterns on the Agulhas Bank. *S. Afr. J. Sci.* 90, 114-122.
80. Sauer W.H.H., Goschen W.S. and Koorts A.S. (1991). A preliminary investigation of the effect of sea temperature fluctuations on squid catches in the inshore areas of the eastern Cape. *S. Afr. J. mar. Sci.* 11, 467-473.
81. Goschen W.S. (1988). *Water circulation and structures in Algoa Bay and*

its environs. M.Sc. thesis, University of Port Elizabeth.

82. Badenhorst J.H. (1974). The morphology and histology of the male genital system of the squid *Loligo reynaudii* (d'Orbigny). *Annls Univ. Stellenbosch Ser. A* 49 (1), 1-36.
83. Von Boletzky S. (1987). Fecundity variation in relation to intermittent or chronic spawning in the cuttlefish, *Sepia officinalis* L. (Mollusca, Cephalo-

poda). *Bull. mar. Sci.* 40, 382-387.

84. Augustyn C.J and Smale M.J. (1989). Cephalopods. In *Oceans of Life off Southern Africa*, eds. A.I.L. Payne and R.J.M. Crawford, pp. 91-104. Vlacberg, Cape Town.
85. Lipiński M.R. (1990). The distribution of cephalopods in South African waters and world-wide. *S. Afr. Comm. Fisherm.* 2, 10-11.

## Community structure, distribution and trophic ecology of zooplankton on the Agulhas Bank with special reference to copepods

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The mesozooplankton of the western Agulhas Bank is largely an extension of the west-coast upwelling community, whereas one copepod species, *Calanus agulhensis*, dominates the eastern Bank community, comprising up to 85% of the copepod biomass. Large populations of this copepod appear to be maintained on the eastern Bank, particularly during spring and early summer, in association with a subsurface ridge of upwelled water. This copepod appears to utilize efficiently the small cells which dominate the phytoplankton assemblage on the Agulhas Bank. Copepods may consume up to 50% of daily primary production. A low food-chain efficiency of < 3% suggests that a large portion of the primary production moves through microheterotrophs. A variety of commercially exploited fish and other planktivores, including invertebrates, compete for copepods as their primary food source. However, considerable research remains to be done to quantify the apportionment of copepods among their predators, and the effects of predation on copepod dynamics.

The Agulhas Bank is the major spawning region for a number of pelagic, demersal and benthic fish species which are economically important in the South African fishery. Pelagic species such as anchovy (*Engraulis capensis*) and pilchard (*Sardinops sagax*) accumulate on the Agulhas Bank during spring and summer. Many of their eggs and early larvae are transported from the western Agulhas Bank to the west coast of South Africa where they recruit to the fishery during autumn and winter.<sup>1</sup> Round herring (*Etrumeus whiteheadi*), hake (*Merluccius capensis* and *M. paradoxus*) and horse mackerel (*Trachurus trachurus capensis*) also spawn on the Agulhas Bank, and utilize the inshore regions on both the west and south coasts as nursery grounds.<sup>2,3</sup> Squid larvae are concentrated on the eastern Agulhas Bank, and drift westwards over the whole Bank as they mature.<sup>4</sup> All of these species consume micro- and mesozooplankton during their early life history, hence the distribution and dynamics of zooplankton are an important component of the trophic interactions throughout the year for both adult and juvenile fish.

The dynamics of the planktonic food web on the west coast are relatively well understood.<sup>5-11</sup> However, comparatively little information has been published on the structure and functioning of the pelagic food web on the Agulhas Bank. Early studies of the zooplankton community in this region were of a descriptive nature. They include work on salps and

doliolids,<sup>12</sup> hyperiid amphipods,<sup>13</sup> Phyllosoma larvae,<sup>14</sup> euphausiids,<sup>15</sup> chaetognaths,<sup>16,17</sup> pelagic tunicates,<sup>18</sup> and on the occurrence of *Physalia*.<sup>19</sup> These taxa have recently been reviewed comprehensively.<sup>5,8,20,21</sup> Quantitative data on the distribution of zooplankton have been collected since the mid-1970s, while studies of secondary production, particularly of copepods, were initiated in 1988 as part of the environmental monitoring programme during hydro-acoustic pelagic-stock assessment surveys of the Sea Fisheries Research Institute.

The objectives of this paper are: (i) to review existing knowledge on the community structure, distribution and abundance of zooplankton, with particular reference to the copepods, and on rates of grazing and secondary production of the dominant copepod species, and (ii) to investigate their trophic relationships within the pelagic realm. For comparative purposes, the Agulhas Bank has been divided into the western Agulhas Bank (WAB) and the eastern Agulhas Bank (EAB), with the division between the two sectors being a line extending from Cape Agulhas (20°E) to the tip of the Bank (Fig. 1). The two net-zooplankton size groups, namely meso- and macrozooplankton, referred to in this paper, are defined as those zooplankton retained by a 200- $\mu$ m mesh net, but only macrozooplankton are retained by a 1 600- $\mu$ m mesh net.

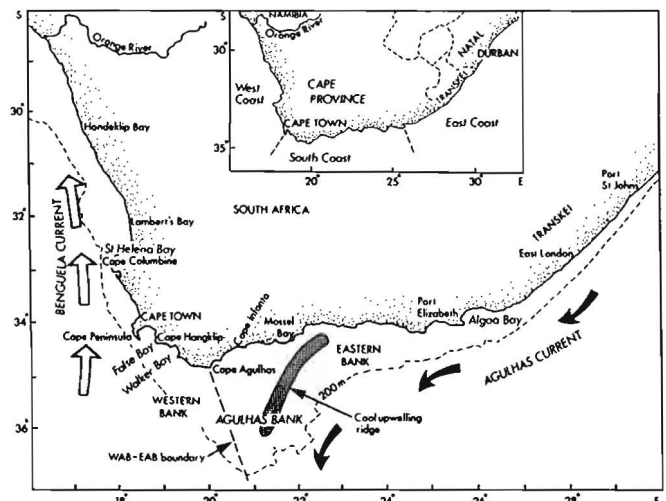


Fig. 1. Southern Africa, showing the Agulhas Bank, the boundary between the western Agulhas Bank and the eastern Agulhas Bank, the position of the cool upwelling ridge, the Benguela and Agulhas Currents and places mentioned in the text.