FISHERIES BIOLOGY, STOCK ASSESSMENT, AND MANAGEMENT OF THE CHOKKA SQUID (*LOLIGO VULGARIS REYNAUDII*) IN SOUTH AFRICAN WATERS: AN OVERVIEW

C. JOHANN AUGUSTYN AND BEATRIZ A. ROEL

Sea Fisheries Research Institute Private Bag X2 Rogge Bay 8012 South Africa augustyn@sfri.wcape.gov.za

ABSTRACT

Extensive studies of biology and life cycle, and the application of some stock-assessment techniques to South African chokka squid (Loligo vulgaris reynaudii) have contributed toward formulating management approaches for the species. Efforts to clarify the systematics preceded the biological, behavioral, population dynamics, lifecycle, and ecological studies. Management measures have progressed from simple ones designed to order the fishery and control effort, to a more structured approach that uses a closed season as the main management tool. Recent modeling studies have indicated that the stocks are nevertheless under pressure, at a time when there is a political imperative to allow new entrants into the fishery. There is consequently a need to introduce new methods of management (while maintaining effort control as opposed to catch control), which may ultimately lead to the introduction of an operational management procedure.

INTRODUCTION

This paper reviews the progress that has been made in South Africa since the early 1980s in understanding the biology and life cycle of chokka squid (*Loligo vulgaris reynaudii*). It describes how this knowledge has been combined with various stock-assessment techniques to develop a management approach for a species that is one of a group considered to be very difficult to manage effectively (Pierce and Guerra 1994).

Until the mid-1980s chokka squid was taken almost exclusively as a bycatch of the demersal trawl fishery. A small-boat, entrepreneurial, handline jigging fishery was established in 1985 (Augustyn 1986). It grew explosively, but was soon brought under licensed control. Today the chokka squid jigging fishery is based on a relatively small (mean catch: about 6,000 metric tons), but valuable resource (close to R 104 million, or \$22 million; Cochrane et al. 1997) which is exploited entirely in South African waters. Catches have fluctuated between approximately 2,700 and 11,000 t per year (fig. 1).

FISHERIES BIOLOGY OF CHOKKA SQUID

Extensive research has been conducted on chokka squid, mostly since the early 1980s. The following aspects have been investigated.

- Morphological and biochemical systematics (Augustyn and Grant 1988; Vecchione and Lipiński 1995)
- Embryological and larval development (Vecchione and Lipiński 1995; Blackburn et al., in press)
- Ageing methods and physiology of statolith deposition (Lipiński 1991, 1993; Lipiński and Durholtz 1994, 1996; Durholtz et al. 1995, 1997; Gerneke et al. 1995; Durholtz and Lipiński 1997; Lipiński et al. 1997; Lipiński, Durholtz, and Underhill, in press)
- Trophic relationships and feeding behavior, feeding physiology (Lipiński 1987, 1990, 1992; Lipiński and David 1990; Sauer and Lipiński 1991; Smale et al. 1995)
- Direct stock-assessment methods, including trawl and hydroacoustic surveys (Hatanaka et al. 1983; Uozumi et al. 1984, 1985; Wallace et al. 1984; Augustyn et al. 1993; Lipiński, Hampton, et al., in press)
- Stock-assessment modeling and methods (Augustyn et al. 1993; Roel et al., in press)
- Management (Augustyn 1986; Lipiński 1990; Augustyn et al. 1992, 1994; Sauer 1995a, b)
- Reproductive histology and fecundity (Badenhorst 1974; Sauer and Lipiński 1990; Peredo et al. 1996; Melo and Sauer 1997, in press)
- Reproductive biology and spawning and schooling behavior (Lipiński 1979; Augustyn 1990; Sauer et al. 1992; Sauer and Smale 1993; Hanlon et al. 1994; Sauer, Roberts, et al. 1997)
- Migration (Sauer et al. 1994; O'Dor, Andrade, et al. 1996; O'Dor, Webber, et al. 1996)
- Short- and long-term environmental effects on availability and spawning (Sauer et al. 1991; Roberts and Sauer 1994; Roberts et al. 1996; Roberts, in press)
- Population dynamics and life-cycle studies (Augustyn 1989, 1991; Sauer 1991, 1993; Sauer et al. 1993; Augustyn et al. 1994; Lipiński 1994; Booth et al. 1997; Sauer, Augustyn, and Roberts 1997)



Figure 1. Annual catches of South African chokka squid (Loligo vulgaris reynaudii) in three sectors, from the inception of the fishery in 1985 to 1997.

Systematics

Several years before the jigging fishery developed, Sea Fisheries Research Institute (SFRI) recognized that chokka squid was a potential new resource. A fisheries biological research project was launched in the early 1980s. Investigating the systematics became a priority because it was realized that, if a fishery were to be established and properly managed, the stock distribution would have to be delimited and its systematic relationship with its European and West African counterpart, L. vulgaris, established. From a study in which morphological measurements, meristic counts, and protein gel electrophoresis were used, it was determined that the South African species was a distinct and isolated one and that genetic differences were at the subspecific, rather than specific level. On that basis, the two species were renamed L. vulgaris vulgaris and L. vulgaris reynaudii (Augustyn and Grant 1988).

Biological Studies

Initially the trawler bycatch was sampled to collect basic biological information in an attempt to understand development, growth, population structure, maturation cycle, and ecology. Later, the spawning grounds in bays along the southern coast of South Africa were investigated (Augustyn 1989). The main spawning sites were then thought to be located in False Bay, near Cape Town. In the early 1980s, the distribution and relative abundance, as well as basic biology and ecology were directly studied for the first time on the shelf, during three joint Japanese–South African surveys of the South Coast Shelf (Hatanaka et al. 1983; Uozumi et al. 1984, 1985). These were soon followed with regular stratified random sampling surveys by a new South African research vessel. The surveys encompassed the whole coast and established an index of abundance (Augustyn 1989, 1991). The distribution of mature animals and different size classes indicated that the main spawning areas were located farther east than had earlier been suspected. Eventually these surveys made it possible to draw a more complete picture of the life cycle, including aspects such as deepwater spawning and larval distribution.

With the onset of a directed jigging fishery on chokka squid, the focus of the research shifted to the southeast coast, because it was realized that the major spawning grounds were located there. Research based on scuba diving clarified the understanding of chokka squid's mating and spawning behavior and of its seasonality and probable life cycle (Augustyn 1990; Sauer 1991). At the same time, the first steps were taken toward using statolith daily growth rings to determine the age of squid and the basis of ring deposition in statoliths (Lipiński and Durholtz 1994, 1996).

In the late 1980s a Squid Working Group at the SFRI in Cape Town was established, and cooperation with the squid industry began to lend new impetus to the research. New work, including migration and tagging studies (Sauer et al. 1994), acoustic studies, and more advanced behavioral studies using acoustic tags (Sauer, Roberts, et al. 1997), as well as a comprehensive environmental research project made further contributions to understanding the population dynamics of chokka squid.

Our current understanding of the life cycle of this squid is summarized by the diagram in figure 2. The species is relatively short-lived, apparently not exceeding a life span of 18 months. The population is usually made up of at least two, sometimes three, major cohorts. Spawning usually peaks in spring and early summer, with a variable smaller peak in autumn or winter (Augustyn 1989, 1990; Sauer 1991). A large part of the population



Figure 2. Conceptual diagram of the life cycle of chokka squid (Loligo vulgaris reynaudii) in its main area of distribution off the south coast of South Africa. TCNP = Tsitsikamma Coastal National Park.

migrates in waves as mature animals to the southeast coast, where most spawn in the shallow (20–50 m) spawning grounds (Augustyn 1989, 1990; Sauer 1991). These variations are reflected in the catches, as shown in figure 3. Availability on the spawning grounds appears to be linked to cool, clear, upwelled water, a seasonal feature at the capes on the southeast coast, which results from easterly wind forcing (Sauer et al. 1991). When waters are warmer than about 21°C or become turbid, the squid tend to spawn in deeper water, often deeper than 100 m. The squid are then less available to the fishery, and different fishing techniques are applied.

Behavioral studies in maintenance experiments in the laboratory, and scuba diving have established that visual



Figure 3. Monthly chokka squid (*Loligo vulgaris reynaudii*) jig catch variations, reflecting changes in availability on the spawning grounds.

signaling with distinct body patterns plays an integral role in spawning and other behavior (see fig. 4), and it is thought that turbid conditions interfere with this behavior.

Different types of shoaling behavior have been identified on the spawning grounds. Spawning squid often form mushroom-shaped aggregations (Sauer et al. 1992). The structure of these aggregations and the movement around them has been elucidated by acoustic tagging studies (Sauer, Roberts, et al. 1997). Several other types of aggregations have also been observed and are characterized by typical echo-sounder trace types (Sauer et al. 1991).

Tagging with "spaghetti" tags has also made it possible to plot longshore movements of squid. Distances of up to 200 km have been measured between tagging and recapture positions, and a generally eastward direction of migration has been established (Sauer et al. 1994).

Lipiński, Hampton, et al. (in press) have studied the stability of individual spawning shoals through tag-andrelease experiments. By comparing several biological parameters, Lipiński (1994) investigated the selectivity of various fishing methods—i.e., jigging, midwater trawling, and purse-seining. Assuming that purse-seining provided the most representative sample of the squid school targeted, jigging proved to be highly selective of large males. No females were caught by this method, whereas the purse-seining ratio of males to females was



Figure 4. Male chokka squid fin and mantle patterns as observed on the spawning grounds (after Sauer and Smale 1993). *a*, Lateral mantle streaks; *b*, all dark; *c*, fin spots; *d*, dark fin edges; *e*, dorsal stripe; *f*, ring pattern.

2.52 to 1. Commercial jig catches do not, therefore, represent the population, and neither do jigged, or to a lesser extent, midwater-trawled research catches. These conclusions obviously have important consequences for stock-assessment methods based on commercial catch data or on research catches.

Acoustic tracking studies have been carried out by Sauer, Roberts, et al. (1997). Squid were tagged (inside the mantle cavity) with acoustic transponders, the signals of which are detected by transducers on a grid of four buoys. The data are radio-beamed ashore to a second receiver linked to a computer which calculates three-dimensional tracks of up to eight squid at a time. The study elucidated movements of male, female, and "sneaker" males. They showed that the squid tend to move off the egg beds at night to feed in the vicinity and that mating mainly takes place during daylight. These studies support the acquisition of baseline data on population dynamics, which are influenced by reproductive behavior. The study emphasized that management strategies should be aimed at avoiding breakdown of these critical spawning aggregations. Recruitment could, for instance, be adversely affected by increases in the alternative tactic of mating and spawning offshore, where development temperatures and success may be lower. Studies of hatching success at various temperatures can therefore also be justified in terms of management advantages.

More recently, a system is being developed to remotely monitor the behavior of squid in relation to environmental parameters by setting up a video camera system linked to a solar-powered surface buoy (fig. 5) which beams the video and environmental data back to shore where it can be stored and later analyzed (Roberts, in press). This work should contribute to understanding the effects of rapid temperature and turbidity and current regime changes on squid availability and behavior.

STOCK ASSESSMENT AND MANAGEMENT

Introduction

Very few squid fisheries around the world are subject to rigorous standard stock-assessment or operational management procedures. This can probably be ascribed largely to the fact that squid are typically annual species with highly variable stock-recruitment relationships and consequently volatile stock levels (Pierce and Guerra 1994). In upwelling systems such as the southern Benguela and the extremely variable south coast of South Africa, the center of the local chokka squid fishery, food availability and survival in the nursery areas are critical to survival and growth, and predicting recruitment is fraught with difficulties. At the same time, many species aggregate strongly and migrate freely, so the use of catch per unit of effort (CPUE) indices (the basis of most population modeling) must take these characteristics into account. On the practical side, data from the fishery are often inaccurate or missing.

In the following sections we review the South African approach to stock assessment and management, which has been modified and adapted as more knowledge has been gained. Over a period of slightly more than a decade, we have moved from a situation of very limited knowledge and expertise into one based on improving knowledge. Higher complexity and more limited resources in terms of surveying and manpower have forced us to take compensatory pragmatic measures. Future options are also touched on briefly.

Direct Estimates of Biomass

Direct population estimation before the start of or during the main fishing season, such as hydroacoustic, stratified random sampling, or egg production surveys



Figure 5. Testing a solar-powered buoy, used to power underwater video equipment that constantly monitors the behavior of chokka squid in the vicinity of egg clusters in response to changes in environmental variables, in South Africa. Photograph reproduced with the permission of Mike Roberts of Sea Fisheries Research Institute, South Africa.

have been used or considered in South Africa (Augustyn et al. 1993). Hydroacoustic methods have not yet been fully developed, and some difficult scientific obstacles still have to be overcome (e.g., how to detect squid when not in large schools). On the other hand, there have been recent successes in directly estimating target strength by using split-beam echo sounders to measure caged squid (M. Soule, pers. comm.).

Stratified random sampling surveys, primarily designed to estimate hake biomass, are currently carried out on the South African south coast in spring and autumn. These surveys also provide estimates of squid biomass, which are useful in determining shelf biomass trends. The surveys do not, however, give an estimate of absolute biomass, because they do not cover the entire area of distribution and because only squid swimming close to the bottom will be caught by the trawl. The proportion missed by the trawl is not known (Augustyn 1991; Augustyn et al. 1993; Roel, unpubl. data). Additional, dedicated squid surveys would be too expensive in terms of vessel time and manpower required, so alternatives for estimating the biomass of the resource are needed.

Practical Management Measures

Since the chokka squid jigging fishery in South Africa began in the mid-1980s, various management measures

have been introduced (Augustyn et al. 1992). These have generally taken cognizance of the biology of chokka squid, but they have also been based on pragmatic decisions made in the absence of good information about the level of squid stocks. An early debate about effort control versus catch control (in about 1989) resulted in the adoption of effort control. The main arguments then were that there was no time series of any length from which to determine trends, and that the life cycle was too short to predict and capitalize on good year classes. A total allowable catch (TAC) could not be set with any confidence, given the absence of a proven survey method. Further, if effort could be kept under control, the fishery would largely ride the good years and survive the poor years.

The first steps to limit effort had, in fact, already been taken a few years earlier, when the developing fishery threatened to spiral out of control. In 1985–86, the fishery was developing explosively as a market was discovered in Europe, and a favorable exchange rate made exports very lucrative. Rapidly declining product quality threatened the market (due to poor handling and freezing practices), and there were even reports of dumping. It was realized that we were dealing with a valuable resource that had to be used sustainably and managed properly. Initial actions were aimed at limiting the hordes of recreational fishermen and favoring the bona fide commercial and semicommercial line fishermen who had developed a catch record over the first two years of the fishery. Those who could demonstrate that they had exceeded the threshold catch levels for each class of vessel were given chokka permits. This resulted in a reduction from more than 500 boats to about 235, of which about 70 were limited to specific areas where they were given rights to catch for bait purposes only. A three-year moratorium on the selling of permits was instituted to prevent short-term profiteering. A public bag limit was set in 1986 (20 squid/person/day). Later, the unit of effort in the fishery became men, and the number of men for each vessel was fixed.

Limitations on vessel size and fishing methods were also considered but discarded, on the grounds that they would lead to inefficient harvesting and therefore introduce economic distortions. Purse-seining was, however, banned outright, being considered too destructive of the spawning habitat. Trawling of spawning squid is also not feasible, because it has been prohibited in all the major spawning areas of squid on the south coast via a ban on trawling in bays since 1987.

Closed Seasons/Areas

Increasing efficiency and declining catch rates of demersal squid bycatch (which reflects abundance of mostly subadults on the shelf) led to a closed season strategy, which reduced effort by shortening the fishing season by several weeks (initially four) and by affording protection to spawning females at the peak of the breeding cycle.

Closing areas, perhaps in cyclic fashion, was also considered. There was, however, already a de facto closed area in the Tsitsikamma Coastal National Park (adjacent to the main spawning areas), and it was necessary to determine its effectiveness by investigating the level of spawning taking place there. Although a thorough evaluation has not yet been completed, there does appear to be considerable spawning activity there. Sauer's (1995b) findings in this regard are unofficially substantiated by occasional prosecution of illegal fishing activities on spawning aggregations within the three-mile-wide national park.

Leslie-DeLury Option

In the early 1990s, the SFRI investigated an effortbased management approach that would allow efficient use of the resource. The possibility of closing the fishery at an appropriate level of escapement, by applying Leslie-DeLury analyses to catch-rate data to determine the peak and subsequent decline of each major influx (Beddington et al. 1990; Rosenberg et al. 1990), seemed a possible option. Its application would have required close-to-real-time monitoring of catch rates each time there was an influx of squid.

The method appears to work well in the Falkland Islands, where the objective of applying a target escapement level is to allow enough squid to escape the fishery at the end of the fishing season so as not to appreciably reduce the probability of good recruitment in the following season. In the South African context, the objective would be to allow sufficient spawning to take place to reach the same goal. In the Falklands the situation is simplified by the fact that a limited number of large vessels supply daily catch (in mass and numbers) and effort data, but in South Africa, almost-real-time monitoring of catch rates on a large number of small vessels would be required (currently beyond our means). The method also works on the assumption of a closed population during the period that the stock is being fished out. Chokka squid populations can display several immigration waves per year (Augustyn 1989; Sauer 1991) and apparently continue to immigrate and emigrate to and from the spawning grounds (the "conveyor belt" concept; des Clers, pers. comm.). As a result, the method was reluctantly rejected as too impractical for the South African fishery. If clear abundance peaks can be defined and a representative sampling method devised (along with rapid collection of data) it does, however, remain an attractive possible future option.

Variable Closed Season

When it appeared that the logistics of the Leslie-DeLury approach were beyond early implementation, the SFRI returned to the closed season as the primary tool of effort management and spawning protection. The closed season was first implemented in 1988, and extended from approximately the last two weeks of October until mid-November. The period coincides with the peak of the spawning season, when squid aggregate inshore and become very vulnerable to the jigging fishery. The duration of the closed season was determined in relation to the perceived resource abundance. The estimate of shelf biomass from the annual spring survey, together with the commercial catch taken in the first seven months of the year, were used as indices of resource abundance after examination of a large number of indices.

A set of decision rules were then put into place to determine the duration of the closed season. This was allowed to vary between three and five weeks, depending on the survey estimate and the catch index (table 1). However, in 1997 it was recommended that the closed season be held at four weeks to allow the implementation of a closed season that would also apply to recreational fishers. This strategy will have to be reviewed in the future.

TABLE 1
Rules for Determining the Duration of the Closed Season
for Chokka Squid in South Africa

Rule	Biomass/catch	Duration of closed season (weeks)
1	Spring biomass < 10,000 t	
	or	
	January–July catch < 500 t	5
2	10,000 t < spring biomass < 20,000 t and	
	500 t < January–July catch < 5,000 t	4
3	10,000 t < spring biomass < 20,000 t and	
	January–July catch $> 5,000$ t	3
4	Spring biomass > 20,000 t and	
	January–July catch > 500 t	3

Dynamic Biomass Modeling

Direct estimates of stock abundance from demersal surveys and catch per unit of effort data from both the demersal fishery and the jig fishery have been used as indices of stock abundance to assess the stock by means of biomass dynamic models. The indices suggest conflicting trends, so they were also combined to estimate initial biomass, growth rates, replacement yield, and depletion rates. The results indicate that a reduction in effort is required in order to prevent the replacement yield from being exceeded, the size of such reduction being very sensitive to model assumptions (Roel and Cochrane 1996).

The results of modeling also show that biological and economic gains provided by the currently applied closed season are relatively small, consistent with an approximately 9% reduction in effort (Roel et al., in press). Although the benefits may be greater at higher levels of effort than those currently being applied, such levels correspond to high risks of depleting the spawning biomass to levels at which the chance of successful recruitment might be impaired. They are therefore not feasible management options, even with a closed season. However, decisions about the desirability of the closed season should not be taken without considering the desirable effort level in the fishery as a whole.

According to Roel et al. (in press), advice on an appropriate level of effort for the fishery at this stage is difficult because:

- 1. Although point estimates indicate that the current level of effort is below that which would lead to maximum yield, the estimates are not precisely determined and therefore need to be interpreted with caution.
- 2. Risk-related statistics (high for the base-case assumptions of these analyses) are very sensitive to the assumptions made in the model and to speci-

fication of the spawning biomass level below which average recruitment is likely to fall. There is little information from squid fisheries elsewhere in the world upon which to base an informed opinion on this matter, other than the work done in the Falklands (Basson and Beddington 1993).

Although, therefore, the closed season seems little more than a mechanism for effort reduction on the basis of the assessment results, it would seem prudent, in view of the apparently high levels of risk associated with the current effort level, to maintain it and to limit the effort permitted in the fishery to the current level until greater clarity on the matters raised in points 1 and 2 above is obtained.

Options in the Near Future

The fishery has reached the mature stage of development when a management procedure could be considered and implemented. A management procedure for squid, as for other stocks, would be a set of clearly defined rules (tested by simulation) specifying:

- 1. How the regulatory mechanism (for example, a total allowable annual effort) is to be set, typically on an annual basis;
- 2. What data are to be collected for the purpose; and
- 3. Exactly how the data are to be analyzed and used to this end.

The set of rules is to be preagreed upon by the parties involved, typically the management agency and the fishing industry. The management procedure should be put into place for a number of years (three to five seem to be an acceptable standard period in most fisheries) and left to run for this period. Thereafter, the procedure should be reviewed and modified as necessary in light of changes in understanding of the resource or the fishery that may have developed in the interim. A revised procedure would then be implemented for the next three-to-five-year period.

At a recent international workshop on cephalopod fisheries held in Cape Town (during the 1997 Cephalopod International Advisory Council Symposium) it became clear that very few fisheries of this nature around the world are managed by catch limitation; in most cases it is fishing effort that is controlled. In the only squid fishery known to operate on a TAC (the U.S. New England trawl fishery on *L. pealei*), the number of vessels is also strictly limited (J. A. Brodziak, pers. comm., 1997). The primary reason for preferring effort control is that, in most cases, setting a TAC is extremely difficult in the case of short-lived organisms such as squid, unless realtime monitoring of the resource biomass is feasible. As a result, management is likely to be faced with two equally unsatisfactory options when setting a TAC: (1) a conservative TAC is set and the resource is protected but often underutilized; or (2) a more risk-prone approach is taken, but the resource could be depleted if conditions for recruitment are unfavorable for a few years in succession.

Alternatively, when the effort is held constant (in terms of vessels and men), the same proportion of the stock would generally be harvested each year, with good years being taken advantage of by the fishing industry, and the necessary protection being provided to the resource in years when the biomass is low. Ideally, some mechanisms should be introduced to reduce fishing pressure on the stock in years when clear signs of poor recruitment can be detected. These could take the form of a shortening of the fishing season or limitation of the annual catch. Another advantage of effort control is that misreporting of catches is seldom a serious factor, because there is little or no incentive for fishers to provide incorrect catch statistics.

There are, however, concerns relating to the implementation of fishing effort limitations. These include difficulties in monitoring changes in effective effort and the costs of enforcing regulations such as, for example, the number of men on board. On the other hand, if catch limitations were to be implemented, problems of monitoring and enforcement would be exacerbated even more.

It has consequently been recommended to the South African management authority that effort control should, for the time being at least, remain the primary management tool for chokka squid. An aim of the proposed new South African fisheries policy is to allow previously disadvantaged new entrants into all fisheries, and strategies for doing so in effort-controlled fisheries such as the squid jigging fishery will clearly require some innovative thinking. Such measures should be aimed at redistributing fishing effort while maintaining the current overall level of effort. Possible options could include: (1) allowing new entrants, but curtailing the total time during which the fishery operates in a year; (2) developing mechanisms that could allow new entrants to obtain fishing permits from the present holders; and (3) restricting the area of operation of permit-holders.

The SFRI's proposed strategy for generating scientific solutions to the challenges posed by the new fisheries policy is to initiate debate on the matter, involving all parties associated with the utilization of chokka squid. Such a debate would include scientists, industry representatives, and other interested parties. The ultimate objective would be the development of a management procedure that strikes a balance between effective and fair utilization based on good knowledge of the stock dynamics and trends. It should allow good use of the abundance peaks in the resource with adequate safety measures to keep the risk of stock collapse at a low level. The South African government's new fisheries policy holds out the promise of a responsible approach toward the use of marine resources, but adequate funding for research and enforcement is required to ensure the future of chokka squid and other resources.

ACKNOWLEDGMENTS

The organizers (particularly Doyle Hanan and George Hemingway) and sponsors of the 1997 CalCOFI meeting, especially the California Seafood Council, are sincerely thanked for their sponsorship of the first author's attendance. We also thank the Director of the Sea Fisheries Research Institute in Cape Town for permission to undertake the visit. We are grateful to our colleagues on the Institute's Squid Working Group for their many enthusiastic contributions to the work described in this overview, as well as to the technical and ships' staff who helped collect the data.

LITERATURE CITED

- Augustyn, C. J. 1986. The squid jigging fishery on the South African south coast. S. Afr. Ship. News Fish. Ind. Rev. 41(5):24, 26.

- Augustyn, C. J., and W. S. Grant 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.
- Augustyn, C. J., M. R. Lipiński, and W. H. H. Sauer. 1992. Can the Loligo squid fishery be managed effectively? A synthesis of research on Loligo vulgaris reynaudii. In Benguela trophic functioning, A. I. L. Payne, K. H. Brink, K. H. Mann, and R. Hilborn, eds. S. Afr. J. Mar. Sci. 12:903–918.
- Augustyn, C. J., B. A. Roel, and K. L. Cochrane. 1993. Stock assessment in the chokka squid *Loligo vulgaris reynaudii* fishery off the coast of South Africa. *In* Recent advances in cephalopod fishery biology, T. Okutani, R. K. O'Dor, and T. Kubodera, eds. Tokyo: Tokai Univ. Press, pp. 3–14.
- Augustyn, C. J., M. R. Lipiński, W. H. H. Sauer, B. Mitchell-Innes, and M. Roberts. 1994. Chokka squid on the Agulhas Bank—life history and ecology. S. Afr. J. Sci. 90:143–154.
- Badenhorst, J. H. 1974. The morphology and histology of the male genital system of the squid *Loligo reynaudii* (d'Orbigny). Annale Univ. Stellenbosch, Ser. A 49(1):1–36.
- Basson, M., and J. R. Beddington. 1993. Risk and uncertainties in the management of a single cohort squid fishery: the Falkland Islands *Illex* fishery as an example. *In* Risk evaluation and biological reference points for fisheries management, S. J. Smith, J. J. Hunt, and D. Rivard, eds. Can. Spec. Publ. Fish. Aquat. Sci. 120:viii + 442 pp.
- Beddington, J. R., A. A. Rosenberg, J. A. Crombie, and G. P. Kirkwood. 1990. Stock assessment and the provision of management advice for the short fin squid fishery in Falkland Islands waters. Fish. Res. 8:351–365.
- Blackburn, S., W. H. H. Sauer, and M. R. Lipiński. In press. The embryonic development of the chokka squid *Loligo vulgaris reynaudii* d'Orbigny, 1845. Veliger.
- Booth, T., W. H. H. Sauer, and M. J. Roberts. 1997. The use of GIS in understanding the life cycle and in biomass estimations of chokka. CIAC Workshop on Cephalopod Ecology and Fisheries Management, Cape Town, 31 August-2 September 1997.

- Cochrane, K. L., D. S. Butterworth, and A. I. L. Payne. 1997. South Africa's offshore living marine resources: the scientific basis for management of the fisheries. Trans. R. Soc. S. Afr. 52:149–176.
- Durholtz, M. D., and M. R. Lipiński. 1997. The influence of temperature on squid statolith microstructure. CIAC Workshop on Cephalopod Ecology and Fisheries Management, Cape Town, 31 August–2 September 1997.
- Durholtz, M. D., M. R. Lipiński, W. J. Przybylowicz, and J. Mesjasz-Przybylowicz. 1995. Structural relations of calcium and strontium in squid statoliths. Proc. Electron Micr. Soc. S. Afr. 25:74.

———. 1997. Nuclear microprobe mapping of statoliths of chokka squid Loligo vulgaris reynaudii d'Orbigny, 1845. Biol. Bull. 193:125–140.

- Gerneke, D. A., M. R. Lipiński, M. D. Durholtz, M. E. Waldron, W. H. Oosthuizen, J. Erasmus, and B. T. Sewell. 1995. The visualization of growth increments. Proc. Electron Micr. Soc. S. Afr. 25:72.
- Hanlon, R. T., M. J. Smale, and W. H. H. Sauer. 1994. An ethogram of body patterning behaviour in the squid *Loligo vulgaris reynaudii* on spawning grounds in South Africa. Biol. Bull. 187:363–372.
- Hatanaka, H., T. Sato, C. [J.] Augustyn, A. [I. L.] Payne, and R. [W.] Leslie. 1983. Report on the Japan/South Africa joint trawling survey on the Agulhas Bank in November/December 1980. Spec. Publ. Mar. Fish. Resource Cent., 73 pp.
- Lipiński, M. R. 1979. Universal maturity scale for the commerciallyimportant squids (Cephalopoda: Teuthoidea). The results of maturity classifications of the *Illex illecebrosus* (LeSueur, 1821) populations for the years 1973–1977. Res. Doc. Int. Commn. NW. Atl. Fish. 79/II/38, 40 pp.
- ———. 1987. Food and feeding of *Loligo vulgaris reynaudii* from St. Francis Bay, South Africa. *In* The Benguela and comparable ecosystems, A. I. L. Payne, J. A. Gulland, and K. H. Brink, eds. S. Afr. J. Mar. Sci. 5:557–564.
- ———. 1990. Changes in pH in the caecum of Loligo vulgaris reynaudii during digestion. S. Afr. J. Mar. Sci. 9:43–51.
- ——. 1991. Scanning electron microscopy (SEM) and chemical treatment. In Squid age determination using statoliths, P. Jereb, S. Ragonese, and S. von Boletzky, eds. N.T.R. - I.T.P.P. Special Publication no 1, Mazara del Vallo, Italy, pp. 97–112.
- ———. 1992. Cephalopods and the Benguela ecosystem: trophic relationships and impact. *In* Benguela trophic functioning. A. I. L. Payne, K. H. Brink, K. H. Mann, and R. Hilborn, eds. S. Afr. J. Mar. Sci. 12:791–802.

. 1993. The deposition of statoliths: a working hypothesis. *In* Recent advances in cephalopod fishery biology, T. Okutani, R. K. O'Dor, and T. Kubodera, eds. Tokyo: Tokai Univ. Press, pp. 214–262.

- Lipiński, M. R., and J. H. David. 1990. Cephalopods in the diet of the South African fur seal (*Arctocephalus pusillus pusillus*). J. Zool., Lond. 221:359-374.
- Lipiński, M. R., and M. D. Durholtz. 1994. Problems associated with ageing squid from their statoliths: towards a more structured approach. Antarctic Sci. 6:215–222.
- . 1996. Identification of daily increments in squid statoliths: the main squid ageing problem. Proc. Microsc. Soc. S. Afr. 26:116.
- Lipiński, M. R., W. J. Przybylowicz, M. D. Durholtz, and J. Mesjasz-Przybylowicz. 1997. Quantitative micro-PIXE mapping of squid statoliths. Nucl. Instr. Meth. Phys. Res. B. 130: 374–380.
- Lipiński, M. R., M. D. Durholtz, and L. G. Underhill. In press. Field validation of age from the statoliths of chokka squid *Loligo vulgaris reynaudii* d'Orbigny, 1845 and an assessment of associated errors. ICES J. Mar. Sci.
- Lipiński, M. R., I. Hampton, W. H. H. Sauer, and C. J. Augustyn. In press. Daily net emigration from a spawning concentration of chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) in Kromme Bay, South Africa. ICES J. Mar. Sci.
- Melo, Y. C., and W. H. H. Sauer. 1997. Ovarian atresia during the sexual cycle in *Loligo vulgaris reynaudii*. Cephalopod International Advisory Council (CIAC) symposium on Cephalopod Biodiversity, Ecology and Evolution. Cape Town. 4–7 September 1997.

-------. In press. Ovarian atresia in cephalopods. S. Afr. J. Mar. Sci. 20.

O'Dor, R., Y. Andrade, W. H. H. Sauer, M. J. Roberts, M. Smale, and D. M. Webber. 1996. Upwelling impact on spawning behaviour of tracked *Loligo vulgaris reynaudii*. Benguela Dynamics International Symposium, Cape Town. 25–27 November 1996.

- O'Dor, R. K., D. M. Webber, W. H. H. Sauer, M. Roberts, and M. Smale. 1996. High resolution, 3D tracking of squid on spawning grounds. *In* Proc. 13th Int. Symp. Biotelemetry, C. Cristalli, C. J. Amlaner Jr., and M. R. Neuman, eds. Fayetteville: Univ. Arkansas Press, pp. 193–198.
- Peredo, S., Y. C. Melo, and W. H. H. Sauer. 1996. Post-ovulatory follicles (corpora lutea) in the ovary of the chokka squid, *Loligo vulgaris reynaudii*. 9th South African Marine Science Symposium, Univ. Cape Town. 21–23 November 1996.
- Pierce, G. J., and A. Guerra. 1994. Stock assessment methods used for cephalopod fisheries. Fish. Res. 21:255–285.
- Roberts, M. J. In press. The influence of the environment on chokka squid spawning aggregations: an approach towards a quantified model. S. Afr. J. Mar. Sci. 20.
- Roberts, M., and W. H. H. Sauer. 1994. The environment, the key to understanding the chokka squid *Loligo vulgaris reynaudii* life cycle and fishery? Antarctic Sci. 6(2):249–258.
- Roberts, M. J., W. H. H. Sauer, W. DeWet, and M. van den Berg. 1996. Fisheries management: developing an environmentally driven predictive capability (EDPC) for the South African squid fishery. *In Proc.*, 2nd World Fisheries Congress, 28 July–2 August 1996, vol. 1, D. A. Hancock and J. P. Beumer, eds., p. 65.
- Roel, B. A., and K. L. Cochrane. 1996. A biomass based assessment of the South African chokka squid. Benguela Dynamics Symposium, Cape Town, South Africa, November 1996.
- Roel, B. A., K. L. Cochrane, and D. Butterworth. In press. Investigation on the effects of different levels of effort and of the closed season in the chokka squid jig fishery. S. Afr. J. Mar. Sci. 19.
- Rosenberg, A. A., G. P. Kirkwood, J. A. Crombie, and J. R. Beddington. 1990. The assessment of stocks of annual squid species. Fish. Res. 8:335–350.
- 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, Univ. Port Elizabeth, 87 pp.
- ------. 1993. The ecology of spawning squid *Loligo vulgaris reynaudii* in the inshore waters of the Eastern Cape. Ph.D. thesis, Univ. Port Elizabeth.
- . 1995a. The impact of fishing on squid spawning concentrations on inshore spawning grounds in the southeastern Cape, South Africa. S. Afr. J. Mar. Sci. 16:185–193.
- ———. 1995b. South Africa's Tsitsikamma National Park as a protected breeding area for the commercially exploited chokka squid *Loligo vulgaris* reynaudii. S. Afr. J. Mar. Sci. 16:365–371.
- 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.
- ———. 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.
- Sauer, W. H. H., and M. J. Smale. 1993. Spawning behaviour of Loligo vulgaris reynaudii in shallow waters of the south-eastern Cape, South Africa. In Recent advances in cephalopod fishery biology, T. Okutani, R. K. O'Dor, and T. Kubodera, eds. Tokyo: Tokai Univ. Press, pp. 489–498.
- Sauer, W. H. H., W. S. Goschen, and A. S. Koorts. 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.
- Sauer, W. H. H., M. J. Smale, and M. R. Lipiński. 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.
- Sauer, W. H. H., C. McCarthy, M. J. Smale, and A. S. Koorts. 1993. A detailed examination of chokker squid (*Loligo vulgaris reynaudii*) spawning grounds in the Kromme Bay, South Africa. Bull. Mar. Sci. 53(3): 1066–1077.
- Sauer, W. H. H., M. R. Lipiński, and C. J. Augustyn. 1994. Migration patterns through tagging experiments. The behaviour and natural history of cephalopods, Naples, Italy, 5–11 June.
- Sauer, W. H. H., C. J. Augustyn, and M. J. Roberts. 1997. The life cycle of *Loligo vulgaris reynaudii*. Cephalopod International Advisory Council (CIAC) symposium on Cephalopod Biodiversity, Ecology and Evolution. Cape Town. 4–7 September 1997.

AUGUSTYN AND ROEL: SOUTH AFRICAN CHOKKA SQUID FISHERY CalCOFI Rep., Vol. 39, 1998

- Sauer, W. H. H., M. J. Roberts, M. R. Lipiński, M. J. Smale, R.T. Hanlon, D. M. Webber, and R. K. O'Dor. 1997. Choreography of the squid's "nuptial dance." Biol. Bull. 192:203–207.
- Smale, M. J., W. H. H. Sauer, and R. T. Hanlon. 1995. Attempted ambush predation on spawning squids *Loligo vulgaris reynaudii* by benthic pyjama sharks, *Poroderma africanum*, off South Africa. J. Mar. Biol. Ass. U.K. 75:739-742.
- Uozumi, Y., H. Hatanaka, T. Sato, [C.] J. Augustyn, A. [I. L.] Payne, 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, 91 pp.
- Uozumi, Y., H. Hatanaka, A. [I. L.] Payne, and [C.] J. Augustyn. 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, 78 pp.
- Vecchione, M., and M. R. Lipiński. 1995. Descriptions of the paralarvae of two loliginid squids in southern African waters. S. Afr. J. Mar. Sci. 15:1–7.
- Wallace, J. H., H. M. Kok, C. D. Buxton, and B. [A.] Bennett. 1984. Inshore small-mesh trawling survey of the Cape south coast. 1. Introduction, methods, stations and catches. S. Afr. J. Zool. 19:154–164.