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ASPECTS OF THE BIOLOGY AND POPULATION DYNAMICS OF THE GEELBEK
ATRACTOSCION AEQUIDENS (CUVIER) (PISCES: SCIAENIDAE)
OFF THE SOUTH AFRICAN COAST

THESIS

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Frontispiece: The geelbek, Atractoscion aequidens.

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ABSTRACT

The geelbek Atractoscion aequidens is an important commercial and recreational linefish species along the South African eastern seaboard. Aspects of its biology and population dynamics were investigated using data collected from various sampling sites along the South African east coast and from catch statistics obtained from both the Sea Fisheries Research Institute (Cape Town), and dealer records. The biological aspects studied included age and growth, reproduction and feeding.

It was established that A. aequidens is a fast growing species with a relatively late age at sexual maturity and a 1:1 sex ratio. Feeding studies revealed that it has become specialized to feed on small pelagic fish.

The South African geelbek stock consists of three distinct age related sub-populations, each representing a particular phase in the life cycle. The sub-adults (1-4 yrs) occur in the South West Cape and feed predominantly on anchovy, Engraulis capensis, which they follow, moving inshore in summer and offshore in winter. The adults (5-9 yrs) undergo a seasonal inshore migration to Natal where they spawn in spring. The dynamics of this migration are strongly influenced by the annual movement of their principal prey viz., Sardinops ocellatus, to that region. As a result the geelbek first arrive in Natal during mid winter. Evidence is also presented to suggest that a significant number of "adolescent" fish (4/5 yrs) undergo limited gonad maturation and a partial migration to at least as far as the South East Cape.

Spawning appears to occur offshore. It is postulated that eggs and larvae are transported southwards by the peripheral waters of the Agulhas Current. After spawning the adults probably remain

offshore and use the current to aid their return to the South and South West Cape, where they spend summer feeding on the Agulhas Bank. Juveniles (<1 yr) first appear in the South East Cape between January and March. They apparently use this region as a nursery area for almost a year before moving southwards to join the sub-adults in the South West Cape. In the South East Cape, the juveniles feed initially on mysids whereafter they switch to anchovies and pilchards.

A preliminary stock assessment using yield per recruit and spawner biomass per recruit models, indicated that despite the current legislation the South African geelbek population is already overexploited. This is largely attributed to high rates of fishing mortality of the migratory adult population. Further management recommendations are therefore proposed. These include a size limit (660 mm FL), derived from an investigation of the interrelationship between natural mortality and somatic growth in a theoretical unexploited cohort, as well as a uniform bag limit for all user groups (5 fish per person per day).

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CHAPTER 1

INTRODUCTION

The geelbek, Atractoscion aequidens belongs to the family Sciaenidae (Order Perciformes). The fish of this family are commonly known as the croakers or drums, as most of them are capable of producing sound using specialized muscles which insert on the wall of the swimbladder (Trewavas 1977, Johnson 1978, Van der Elst 1981). The taxonomic status of the geelbek, within the sciaenid family has been unclear since the original description by Cuvier (1830) who placed it in the genus Otolithes. Gill (1863) established the genus Atractoscion to include A. nobilis from the Californian coast and A. aequidens. Jordan and Everman (1898) described Atractoscion as a subgenus of Cynoscion, but Trewavas (1977) re-established the genus Atractoscion to include A. aequidens and A. nobilis, based on the fact that these two species lack the adult canines typical of other Cynoscion species. The classification of Trewavas (1977) is now generally accepted (Heemstra 1986).

Largely because of the earlier uncertainty as to the taxonomic status of the geelbek there exists a considerable synonymy, viz. Otolithes aequidens (Cuvier), Otolithus atelodus (Gunther), Atractoscion atelodus (Gunther), Otolithus teraglin (Macleay), Cynoscion atelodus (Roughley) and Zeluco atelodus (Whitley).

The geelbek is an elongate robust fish (see Frontispiece). It has a lunate caudal fin, a pointed head and a large terminal mouth with several rows of posteriorly pointing needle shaped teeth and a projecting lower jaw. The dorsal and lateral surfaces are silvery grey with a bronze blue sheen which is more prominent dorsally and may become coppery towards the head. The ventral surface is white and the fins are a translucent yellow grey. A black auxiliary spot occurs at the base of each pectoral fin. The most conspicuous feature of this fish is the bright yellow oral cavity from which the name geelbek (yellowmouth) was

derived. This yellow colour extends posteriorly to the inner surfaces of the operculae. There do not appear to be any external differences between the sexes. Detailed taxonomic descriptions of this species are given by Smith (1977), Trewavas (1977) and Heemstra (1986).

The geelbek occurs in all three major oceans and has been recorded off the African as well as the Australian continents (see Fig. 1). On the west coast of Africa it has been recorded from the Arguin Bank in the north (De Groot & Nijsson 1971) and from the Gulf of Guinea southwards to Cape Agulhas (Fischer et al. 1981, Van der Elst 1981). On the African east coast geelbek have been recorded from Cape Agulhas to southern Mozambique (Van der Elst 1981, Fischer & Bianchi 1984) and also in the Gulf of Aden (Druzhine & Filatova 1979).

In Australia A. aequidens has been found off the coasts of New South Wales and Southern Queensland (Roughley 1953, Marshall 1964, Fischer et al. 1981). Their rather extensive distribution has resulted in several common names. In South Africa they are known as geelbek or Cape Salmon, in Australia as teraglin or silver jewfish and in Angola as corvina.

The geelbek is essentially an offshore species which occurs over both sandy and rocky substrata between depths of 15 and 200 m (Roughley 1953, Van der Elst 1981, Fischer et al. 1981). They are not always associated with the substratum and are frequently captured well off the bottom, often close to the surface (Roughley op. cit., Grant 1965, Smith 1968, Anon. 1980, personal observations and communication with fishermen).

Along the South African east coast the geelbek is an important commercial and a highly prized recreational linefish species (Smith & Smith 1966, Smith 1968, Anon. 1980, Van der Elst 1981, Crawford & Crous 1982, Smale 1985). It appears, however, that catches have declined dramatically during the present century (Biden 1930, Smith 1968, Anon. 1980). This is verified by an

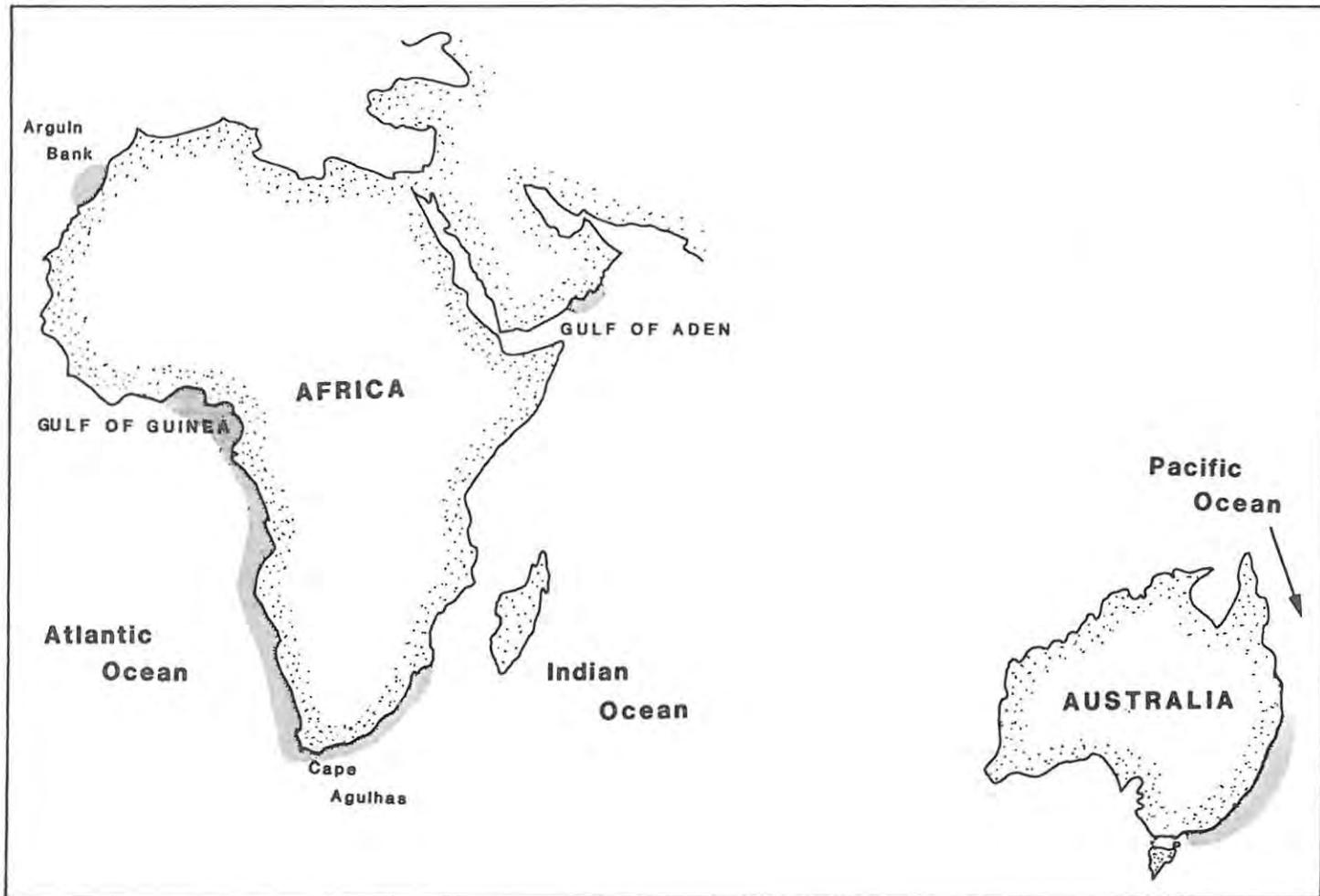


Figure 1. The world distribution (shaded areas) of Atractoscion aequidens.

analysis and comparison of annual catch statistics recorded by Gilchrist (1898-1907) and unpublished data obtained from the Sea Fisheries Research Institute (SFRI) in Cape Town (see Table 1).

Table 1. The mean annual catches and catch per unit effort (C.P.U.E.) of *Atractoscion aequidens* in the South West Cape during the periods 1897-1906 and 1985-1986.

Period	1897-1906	1985-1986
Mean annual catch (tons)	998.12 \pm 25.26	109.73 \pm 7.54
C.P.U.E. (kg/man/year)	1383	30

It is important to note that this decline in the catches has occurred despite technological advances such as nylon lines, marine motors, electronic navigation aids and fish finders. A second point of relevance is that Struisbaai, where approximately 40 per cent of the 1985-1986 geelbek catch for the S.W. Cape was landed, made a negligible contribution towards the catches at the turn of the century. The most likely explanation for this phenomenon was that the Struisbaai Banks had not yet been discovered and were possibly out of the daily range of the row boats used in those days.

Further comparison using the same data sources showed that annual geelbek catches in the entire Cape Province totaled 2,6 times that of another sciaenid, the kob (*Argyrosomus hololepidotus*), which is caught on similar fishing grounds. In contrast to the above, the catches of kob during the period 1985 - 1986 amounted to five times the weight of geelbek landed in this area. It could be argued that the present situation is due to an increase in the abundance of kob. This is, however, unlikely.

Contrary to the expectation that declining catches would have

elicited a research response, surprisingly little was known of the biology of this valuable linefish prior to the initiation of this project (Meyer-Rochov 1972, Van der Elst 1981, Wallace & Van der Elst 1983, Smale 1985). Effective management has therefore been difficult, if not impossible. A comprehensive literature search and communication with J. Pepperell (Fisheries Research Institute, New South Wales, Australia) and M. Cappo (Institute of Marine Science, Queensland, Australia) have revealed that little or no biological information existed for this species in any of the other countries throughout its distributional range.

There is a considerable body of evidence to suggest that the geelbek population off the South African eastern seaboard is separated from the stock off Angola. Rapson et al. (1945), Da Franca et al. (1970) and Penrith (1978) have all reported that the abundance of the Angolan stock decreases southwards with declining water temperature, and that the presence of geelbek off the S.W. African and South African west coasts (north of Cape Point) is a rare occurrence. The second point is further exemplified by Smith (1968), and by Figure 3 in Chapter 2 which shows that essentially no geelbek were landed on the South African west coast between Cape Point and Port Nolloth during 1985 and 1986.

On the South African eastern seaboard A. aequidens is caught all the way from Cape Point to Natal (Van der Elst 1981, personal observations, see also Fig. 3). However, prior to this investigation, it was not known whether those fish comprised a single stock, or in fact consisted of numerous discrete stocks. As exemplified by Cushing (1981) and Gulland (1983) stock delineation is an essential prerequisite for a successful management policy.

The objectives of the present study were to establish whether the South African geelbek comprised a single stock and to obtain an understanding of the biology and population dynamics of the species, in order to formulate a more scientifically based

management strategy for its conservation.

The seasonal occurrence of geelbek in different areas within its distributional range (Robinson & Dunn 1923, Roughley 1953, Marshall 1964, Da Franca et al. 1970, Van der Elst 1981, Smale 1985) implied that this species is migratory. Because information on migration is regarded to be critical for stock separation (Cushing 1981) and to the understanding of the general biology and dynamics of a species (Harden-Jones 1968, McKeown 1984) the theoretical migratory nature of A. aequidens formed the central theme of this investigation.

In Chapter 2 of this thesis the physical oceanography of the South African east coast is briefly reviewed, and the study area as well as the general field sampling procedure is described. The migratory nature of the geelbek is investigated in Chapter 3. Chapters 4 to 7, respectively, cover studies on the age and growth, the reproduction, the feeding and a stock assessment of the geelbek. Concluding remarks and management recommendations are presented in Chapter 8.

CHAPTER 2

COASTAL OCEANOGRAPHY, THE STUDY AREA AND FIELD SAMPLING PROCEDURE

2.1 Coastal Oceanography

Knowledge of the physical marine environment is a prerequisite to the understanding of fish migrations (Lynn 1984). Those aspects of coastal oceanography which were considered relevant to the life history of A. aequidens are described below.

The Continental Shelf

The boundary of the continental shelf is generally taken as the 200 m depth contour line (Branch & Branch 1983) and is shown in Figure 2. Between the South African north eastern border and East London, the shelf is typically narrow, varying between 3,6 and 45 km (Flemming 1978). From this point it begins to widen to form the Agulhas Bank (Fig. 2) which has a maximum width of approximately 250 km (Bang 1973).

The Agulhas Current

Currents generally play a crucial role in the migrations and life histories of migratory fishes (Harden-Jones 1968, 1984, Leggett 1984, Lynn 1984, McKeown 1984).

The southward flowing Agulhas Current (Fig. 2) is a prominent feature of the South African east coast. It is a typical western boundary current and as such has a profound influence on the coastal environment and its biology (Heydorn *et al.* 1978, Schumann 1987). The Agulhas Current is derived mainly from a unison of waters of the South Equatorial Current which flows down the Mozambique channel and the east coast of Madagascar (Bang & Pearce 1978). It then meanders along the edge of the continental shelf initially remaining close to the coast, whereafter it is

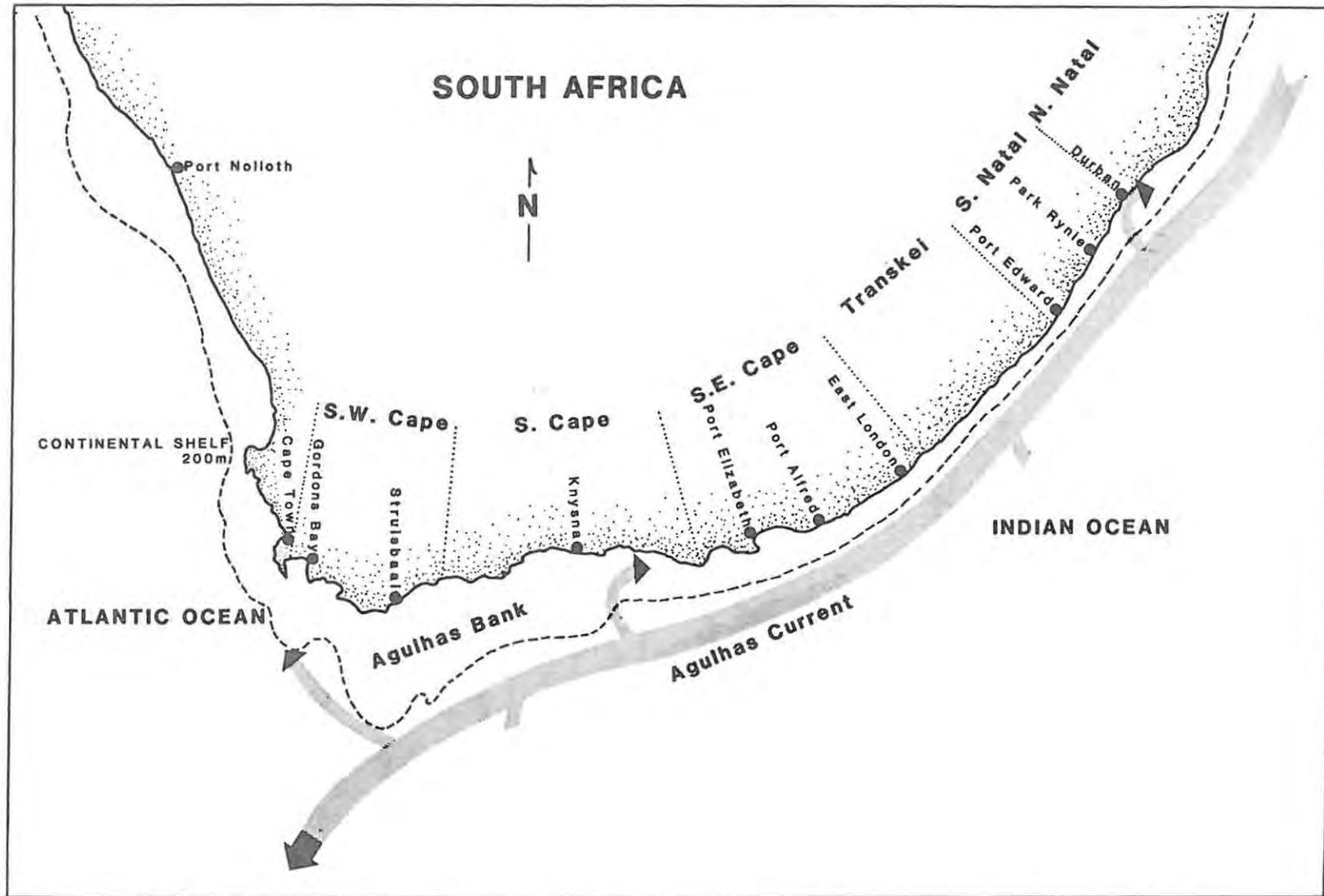


Figure 2. Map of South Africa showing the continental shelf, the Agulhas Current, the division of the eastern seaboard into six coastal regions, and various sampling sites.

deflected out to sea by the Agulhas Bank (Lutjeharms 1981, Schumann 1987). For most of the time it is characterized by a high speed central "core" flowing at more than 1 m/s, decreasing gradually on either side (Grundlingh 1983). The width of the current (taken between the 0.5 m/s isotachs) has been measured at approximately 100 km off Durban (Pearce 1977). Where the current flows close to the coast the coastal waters move in sympathy (Bang & Pearce 1978). However, where the coast and the current diverge, due to meanders, bights and embayments, clockwise vortices, cyclonic eddies and counter currents are often induced (Harris 1978, Schumann 1982, 1987). These may also be influenced by atmospheric pressure and the strength and direction of the prevailing wind (Grundlingh 1974, Bang & Pearce 1978, Harris 1978). Counter currents are a sporadic feature of the coastal waters and earlier speculations of a continuous inshore winter counter current (eg. Mallery 1961, in Baird 1971) have been discounted (Bang & Pearce 1978, Schumann 1987).

2.2 The Study Area

For the purpose of the present study the South African eastern seaboard was divided into six coastal regions (Fig. 2). Regional boundaries were chosen according to those used by the SFRI for assimilating linefish catch data. (The term "eastern seaboard" is used here to incorporate the area from Cape Point to northern Natal).

During a 30 month period from March 1985 to August 1987 biological and length frequency data were collected from Gordons Bay and Struisbaai in the S.W. Cape, Port Alfred on the S.E. Cape coast and Park Rynie and Port Edward on the Natal south coast (see Fig. 2 for geographical localities).

While based in Port Alfred, field trips were undertaken to Natal during September and October of 1986 and to the S.W. Cape during January and February of 1986 and January of 1987. These were planned according to the seasonal abundance of geelbek in these

three regions. The particular sampling areas were selected because they were better frequented by geelbek than other areas (see Fig. 3). Due to a combination of time limitations, the sporadic occurrence of geelbek and the relatively minor catches, no field trips were planned to either the Transkei or the Southern Cape.

2.3 Sampling Strategies and Methods

Difficulties in obtaining whole fish for biological sampling often arose as a result of the sporadic nature of geelbek catches and characteristics inherent to the line fishery in the various areas. This problem was overcome to varying extents by the development of area specific strategies.

In the False Bay area and around Cape Hangklip geelbek were generally caught during the night and sold ungutted in the morning to fish shops in the Gordons Bay vicinity. The strategy for this area simply involved daily contact with the owners of the shops who agreed to hold fish and provide facilities for their examination.

All fish caught in the Struisbaai area were gutted at sea. Fish shop owners agreed to arrange for fishermen to land ungutted fish, provided that the gut mass was paid for. To guard against being inundated with tons of ungutted fish and unaffordable expense these instructions could only be issued to a maximum of two boats daily. However, when geelbek were caught they were most often taken by the non-instructed fishermen. Because of these complications most biological data were therefore obtained from the Gordons Bay area.

Fish caught by the Port Alfred commercial fishermen were all conveniently gutted at a communal jetty. However, due to the fact that fishermen were unwilling to mention geelbek catches over the radio, it was necessary to check on catches every time the boats returned from the sea. Periods of absence were covered

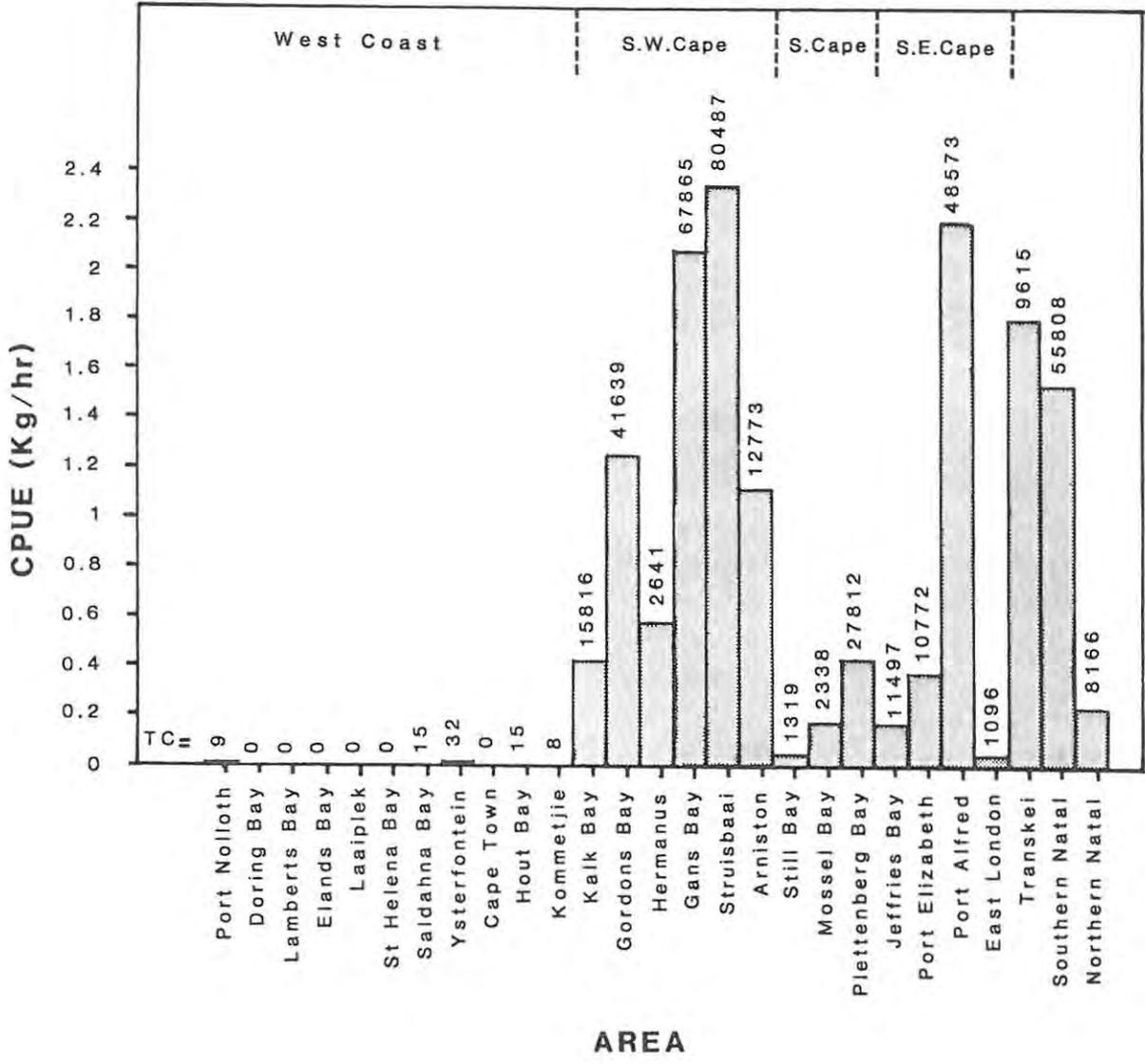


Figure 3. Average catch per unit effort (Kg/hr) (as calculated from SFRI linefish records) for Atractoscion aequidens landed during 1985 and 1986 at consecutive geographic localities along the South African coast. The TC values indicate the total catches (Kg) from each area during the two year period .

by colleagues or assistants.

Sampling problems were initially encountered in Natal as a result of the numerous launching sites along the coast and the fact that fish were quickly gutted on the beaches. However, most of the Natal boats maintained radio contact with either the owners or a central base. It was therefore possible to find out if, where and when boats would be arriving with geelbek. Prospective boats were then met on the beaches and the catches were sampled.

For biological samples the fish were measured for fork length (FL) and total length (TL) in mm and weighed, using certified Salter spring balances, to the nearest 50 grams if they were over five kilograms or to the nearest 10 grams if they were under this weight. They were then cut open, sexed and the gonads were assigned a visual index of maturity, based on a seven point scale (see Chapter 5). Large quantities of fat were often found to be associated with both male and female gonads (see Figs 17, 20 & 21). This was dissected out together with the gonads which were then weighed to the nearest 0,1 g, both before and after fat removal. Stomachs containing food were removed and their contents analysed fresh. Otoliths were extracted for ageing purposes by cutting away a portion of bone from the prootic-exoccipital region (Fig. 4). They were then lifted from the skull with a pair of forceps and stored dry in cross-referenced envelopes.

Time limitations and anxious fishermen often prevented the biological sampling of all landed geelbek. During such occasions the remaining fish were measured for fork length only. Additional length measurements were also obtained from geelbek held in the cold rooms of the various fish shops in Port Alfred and along the S.W. Cape coast.

Fork length measurements for southern Natal and the S.W. Cape were supplemented by data from the Oceanographic Research Institute (ORI) in Durban (n=932) and the SFRI in Cape Town

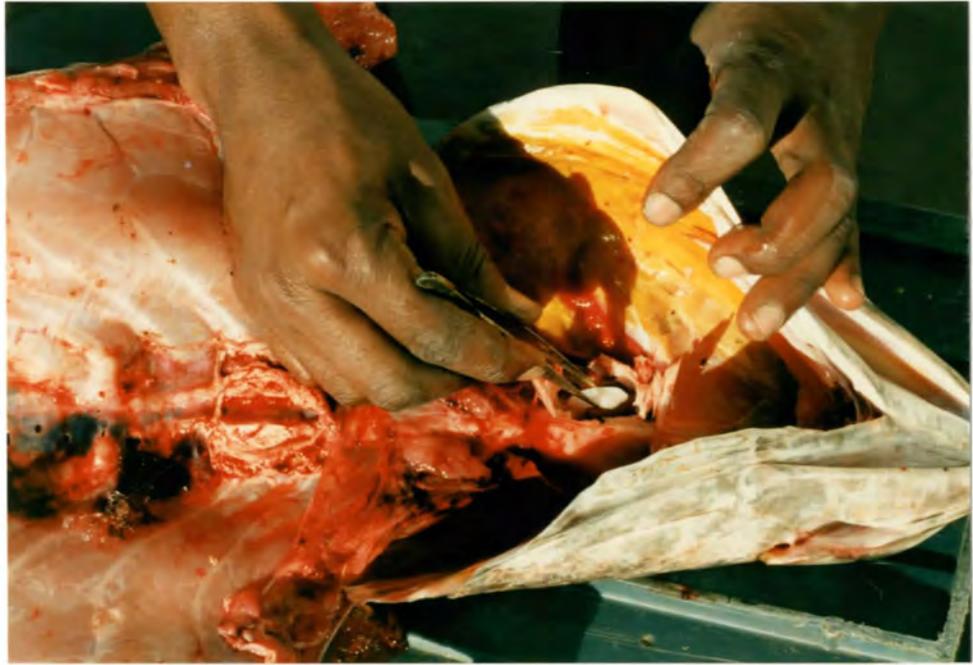


Figure 4. Otolith removal. Note also the distinctive yellow colouration of the gill chamber.

(n=1079).

Although no planned field expedition was undertaken to the South Cape coast, 30 fish were measured for length during an impromptu trip to Knysna in March 1987.

CHAPTER 3

MIGRATION

3.1 Introduction

Decisions on whether specific animal movements represent migrations have been highly controversial in past decades (see Baker 1982). This is largely due to the restrictive nature of earlier definitions of the subject (McKeown 1984). Definitions of the migration phenomenon have, however, become broader in recent years, and at present encompass most animal movements. Baker (1978, in Baker 1982) defines migration as "the act of moving from one spatial unit to another". This definition was adopted for the purposes of the present study.

Migrations may generally be divided into three kinds: gametic, for reproductive purposes; climatic, to secure more suitable environmental conditions; and alimential, for the procurement of food (Nikolskii 1963, Harden-Jones 1968). As pointed out by Van der Elst (1976) more than one type may be operative at any one time.

According to Harden-Jones (1968) studies of fish migrations may be divided into those that set out to describe migrations and those that attempt to explain them. This chapter is primarily concerned with a description of the distribution and movements of A. aequidens along the South African eastern seaboard. Explanations are dealt with in subsequent chapters and are summarised in the final one.

The migratory patterns of A. aequidens were investigated by monitoring temporally and spatially related changes in the size composition and the abundance of catches along the South African coast. This general approach has been used to study the movements of other marine species. These include Engraulis capensis (Crawford 1981a), Sardinops ocellatus (Crawford 1981b,

Armstrong et al. 1987), Pomatomus saltatrix (Van der Elst 1976) and 88 species found in South Carolina estuaries (Shealy et al. 1974).

Estimates of abundance have proved to be particularly useful for investigating the movements of fish. Over and above the previously mentioned examples they have also successfully been used in studying the migration of cod, Gadus morhua (Graham 1924, in Harden-Jones 1968), European hake, Merluccius merluccius (Hickling 1927, in Harden-Jones 1968), herring, Clupea harengus (Marty 1959, in Harden-Jones 1968) and the snoek Thyrsites atun (Crawford & De Villiers 1985).

3.2 Materials and Methods

Size Composition

The size composition of geelbek catches from various regions along the South African coast were investigated using length frequency analysis. A transformation of the von Bertalanffy growth (VBG) equation from Chapter 4 was then used to estimate the ages of fish within these regions. It must be stressed that the 1985 S.E. Cape measurements were not entirely random as biological data were of primary importance during the initial stages of this project. During that year an attempt was made to obtain equal representation for all sizes within the range of lengths observed. Consequently the smaller size classes (<500 mm FL) were under-represented while those in the mid range (510-810 mm FL) were slightly over-represented. These data did however give an indication of the size classes that were and were not present in this area. Due to the relatively low number of fish measured in the S.E. Cape during 1985, they are not believed to have significantly biased the calculations based on regional totals.

Estimates of Catch Mass

Two sources of catch estimates were used for the present study, viz. catch returns and dealer records. As a result of legislation passed in 1984 (Anon. 1984) commercial fishermen have been compelled to submit daily catch returns to the SFRI. As calculated in Chapter 7, this user group is responsible for approximately 85% of the South African geelbek catch. It was therefore possible to obtain fairly accurate monthly estimates of the catches of A. aequidens made in each region during 1985 and 1986. For each region the catches for both years were totalled on a monthly basis and then expressed as percentages of the combined 1985/1986 catch.

Records of the weight of geelbek sold in Struisbaai and Port Alfred were procured from several dealers in the respective areas. In the case of Struisbaai these were obtained indirectly via the SFRI who have been collecting dealer returns from this area since 1975. In Port Alfred the relevant data were acquired by examining the daily receipt books, from 1982 to 1986, of all the dealers in the area. It is important to note that in the Port Alfred area only those fish above 2 kg were recorded, which essentially excludes all those fish from the first mode of the S.E. Cape's bimodal length frequency distribution (see later). In the case of each area the data for all years were combined on a monthly basis. As in the previous section, the totals for each month were expressed as percentages of the total catch.

3.3 Results and Discussion

Annual length frequency distributions for A. aequidens measured in the various regions along the South African east coast are given in Table 2. The length frequency distributions of geelbek measured during the period from 1984 to 1987, for the S.W. Cape, the S.E. Cape and S. Natal are illustrated in Figure 5. Figure 6 shows the monthly length frequency distribution of geelbek measured in the S.E. Cape.

TABLE 2. Annual percentage length frequency distributions for Atractoscion aequidens from various regions along the South African eastern seaboard.

SIZE CLASS (30 mm)	R E G I O N									
	S.W. CAPE			S. CAPE	S.E. CAPE			S. NATAL		
	1985	1986	1987	1987	1985	1986	1987	1984	1985	1986
270-299					0,2		0,1			
300-329					0,7	0,5	0,26			
330-359					3,8	1,1	0,5			
360-389				40,0	4,5	1,8	0,3			
390-419				13,3	7,0	2,1	4,0			
420-449			0,2	20,0	12,7	10,0	20,1			
450-479	0,5		0,5	10,0	7,0	23,6	12,1			
480-509	6,0	4,3	4,5		3,0	13,3	9,0			
510-539	19,0	7,1	14,0		6,2	8,8	5,0			
540-569	16,0	12,8	15,5		1,7	4,0	3,4			
570-599	8,7	10,0	9,6		2,0	1,0	2,0			
600-629	6,3	4,2	6,1		3,0	1,8	0,8	1,0	1,0	
630-659	1,5	11,5	6,0		1,0	1,5	0,5			
660-689	1,0	13,7	7,3		2,0	2,0	0,4			
690-719	1,0	10,1	8,8		0,7	0,4	0,5			
720-749	3,0	7,5	7,7		0,7	0,4	0,3	1,0		
750-779	5,1	5,7	5,5		0,7	0,4	0,3			
780-809	8,3	2,8	4,0		1,2	1,4	0,3			1,3
810-839	9,5	4,3	4,7		1,0	1,7	0,7			
840-869	4,6	2,8	3,2		3,6	3,7	1,6	0,4		2,7
870-899	2,4	1,4	1,3		3,4	4,8	3,7	3,1	1,0	4,4
900-929	2,8		0,6	3,3	2,6	5,0	5,4	14,7	3,2	19,6
930-959	1,9		0,3	6,3	5,3	3,2	8,0	25,0	13,0	33,5
960-989	0,6		0,1	6,3	11,8	5,1	7,8	33,0	23,7	20,0
990-1019	1,1				9,6	3,3	7,2	17,1	19,4	12,0
1020-1049	0,9				4,0	1,7	4,1	5,0	11,8	4,5
1050-1080					0,2		0,8	1,2	4,3	
n =	1079	70	1328	30	415	885	1575	678	93	224

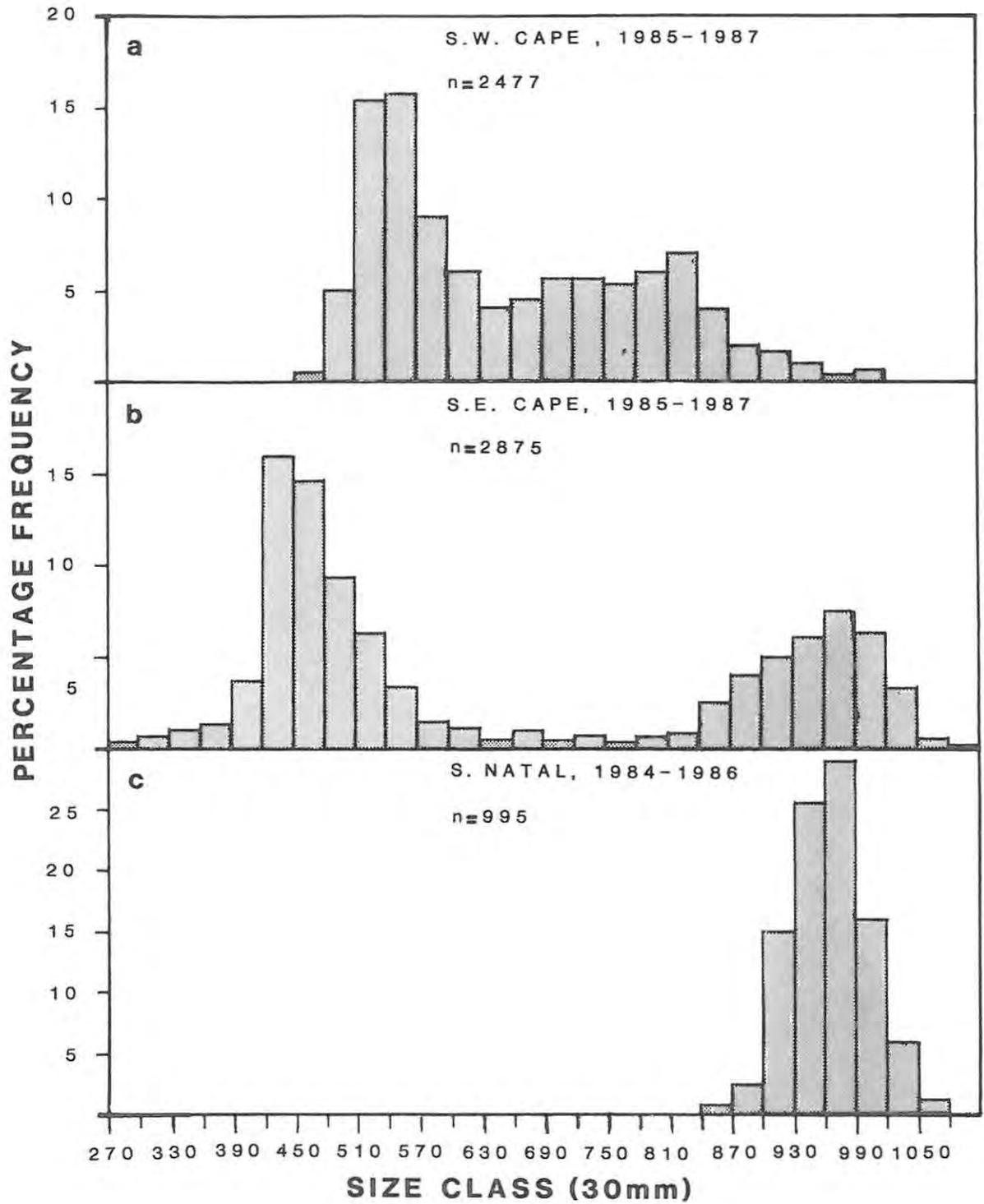


Figure 5. Fork length frequency distributions of *Atractoscion aequidens* from a) the South West Cape, b) the South East Cape, and c) South Natal, 1984-1987.

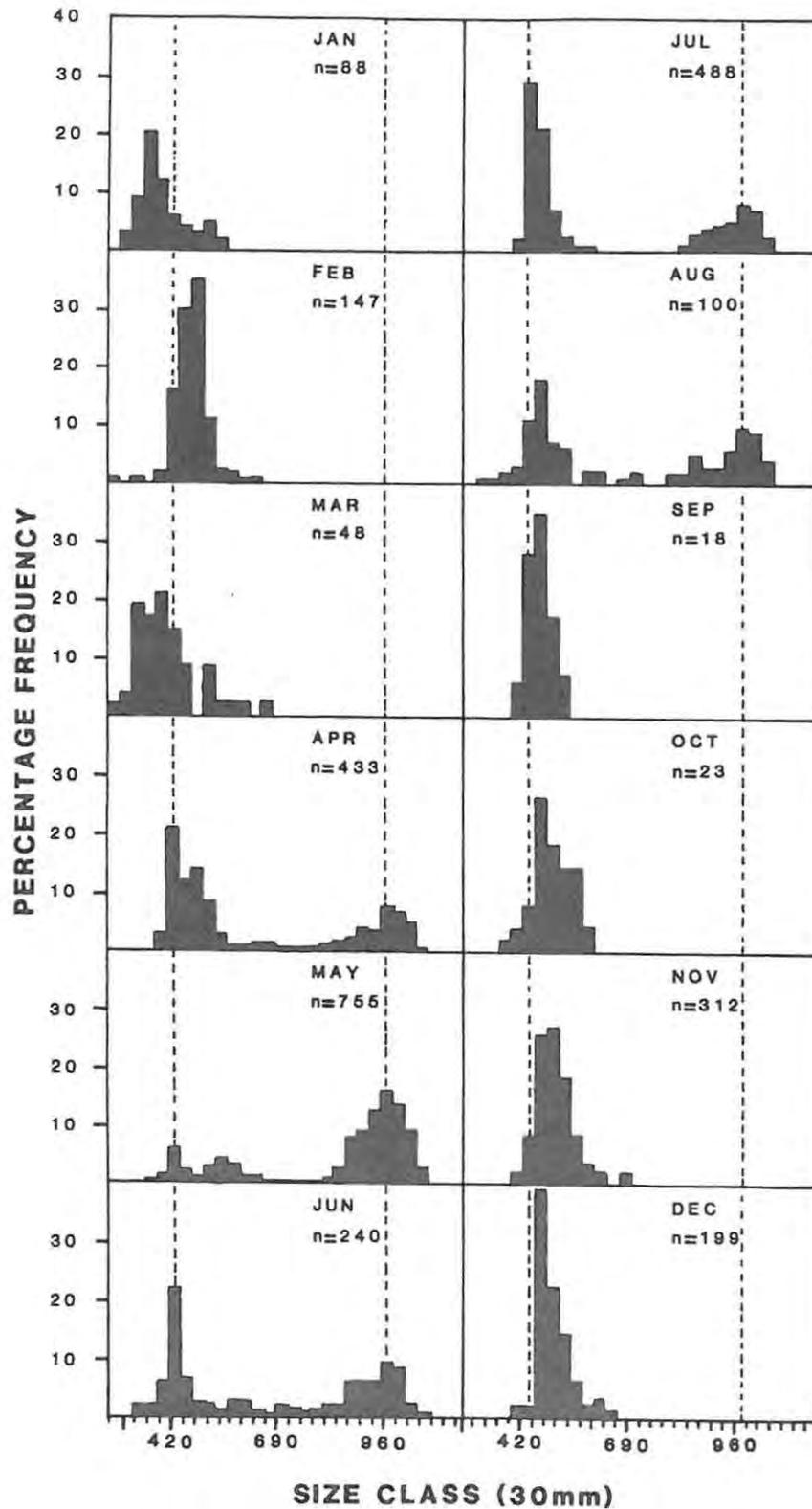


Figure 6. Monthly fork length frequency distributions of *Atractoscion aequidens* from the S.E. Cape, 1985-1987. The dotted lines are drawn through the two size classes which, as shown by Figure 5, represent modal peaks in the S.E. Cape's bimodal length frequency distribution. They are intended as reference points when comparing the length compositions of the monthly catches.

Figure 5b clearly shows that the fish in the S.E. Cape have a bimodal length frequency distribution. The first peak corresponds with the 420-450 mm size class and the second peak with the 960-990 mm size class. Calculations using the VBG equation showed that the fish comprising the first mode (390-540 mm FL) were mainly less than one year old, while those of the second mode (840-1050 mm FL) were between four and nine years of age.

As illustrated by Figure 5a the fish from the S.W. Cape generally belonged to size classes between the two modes of the S.E. Cape, consisting predominantly of fish between 510 and 870 mm FL, and between the ages of one and four years. Smaller and larger fish were poorly represented in that region.

Figure 5c shows that geelbek caught in S. Natal had a length distribution which was almost identical to the second mode of the S.E. Cape, although the fish in the 810-900 mm FL size range were slightly less well represented.

Although only a small number of fish were measured in the S. Cape, Table 2 shows that they had a similar length frequency distribution to those of the S.E. Cape. This table also shows that the regionally specific length frequency distributions illustrated in Figure 5 were substantiated on an annual basis. To maintain this state of dynamic equilibrium it is necessary for the 0-1 year old fish of the S.E. Cape to migrate to the S.W. Cape where they must spend three or four years before returning to the S. Cape and the S.E. Cape or Natal.

The occurrence of geelbek less than one year old in the S. and S.E. Cape and their absence from both Natal and the S.W. Cape (see Table 2 and Figure 5) would imply that the former two regions might function as a nursery area. Communication with fishermen in the Transkei has indicated that fish caught in this region are chiefly of a "large size", comparable to those from S. Natal.

Figure 6 revealed that while fish comprising the first mode of the S.E. Cape's bimodal length frequency distribution were present throughout the year, geelbek of less than 420 mm FL were only present in significant numbers during the period from January to March. During this period in each of the three years of this study, fishermen in the S.E. Cape have reported the existence of "thousands" of geelbek which, as measured from marks made on gunwales and fishing equipment, were around 170 mm to 300 mm FL. Being considerably smaller than the legal size limit (378 mm FL), these large shoals of small fish were not exploited. It therefore follows that fish below 390 mm FL in the S.E. Cape are under-represented in Figure 5b. This is partly substantiated by Buxton et al. (1984) who have trawled geelbek between 72 and 393 mm FL in the S.E. Cape region, and by monthly sampling trips at Port Alfred.

Table 2 shows that fish of less than 420 mm FL were also present in the S. Cape during March. It could therefore be concluded that geelbek smaller than 420 mm FL first appear in the linefishery in the S. and S.E. Cape during the period January to March. The general increase in the size of recruits in the S.E. Cape, as they pass through the year from January to December (Fig. 6), supports the assumption that this region functions as a nursery area.

Finally, the 4-9 year old fish, ie. the second mode of the S.E. Cape's bimodal size distribution, were only present in this region from April to August (see Figure 6).

Figure 7 illustrates the monthly percentage catches of geelbek in five of the six regions along the South African eastern seaboard. Due to the paucity of data from the Transkei this region was omitted. Figure 8 illustrates the monthly percentage catches of geelbek made in Struisbaai and Port Alfred.

Both of the above figures indicate that geelbek occur seasonally in the S.W. Cape, with the highest catches made between December

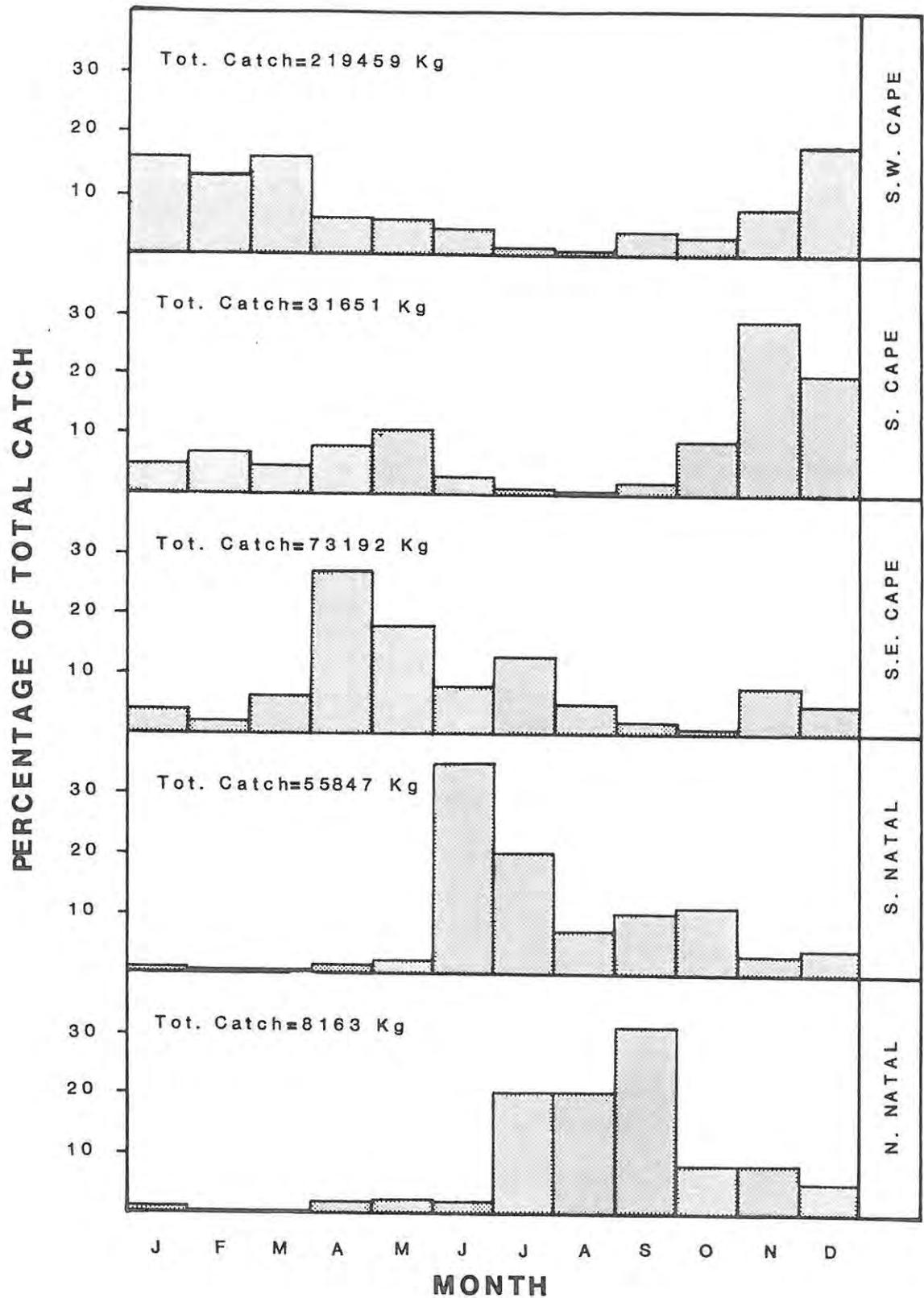


Figure 7. The monthly catches of *Atractoscion aequidens* for 1985 and 1986 expressed as percentages of the total catch for each of five coastal regions. The total catches recorded from each region during the two year period are also given.

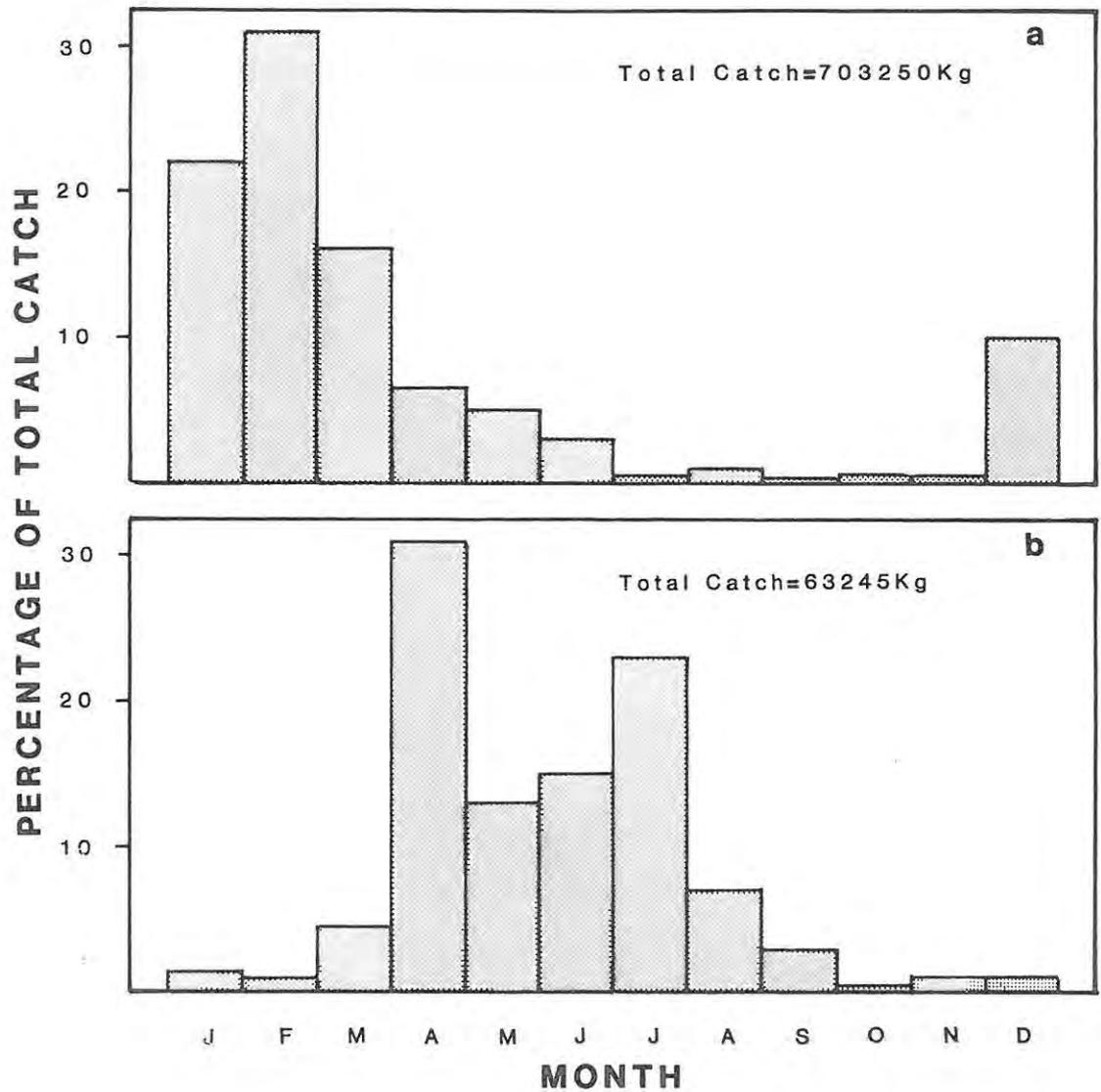


Figure 8. Sum of the monthly catches of *Atractoscion aequidens* expressed as percentages of the grand total for a) Struisbaai (1975-1986) and b) Port Alfred (1982-1986), as calculated from dealer records. The total catches recorded in each area during the respective periods, are also given.

and March. This observation is in agreement with Robinson and Dunn (1923) who designated January, February and March as the best months for geelbek in this region.

Although significant catches of geelbek were made in the S. Cape from October to June, November and December appear to have been the best months for this species (see Fig. 7). Unfortunately insufficient length measurements have precluded an analysis of the sizes of geelbek occurring in this region at different times of the year.

Using the length/weight relationship (see Chapter 4) it was established that the fish of the second mode of the S.E. Cape length frequency distribution weigh approximately 12 times more than those of the first mode. It therefore follows that the abundance analysis illustrated by Figure 7 was heavily biased towards the occurrence of the larger individuals in this region. Figures 6, 7 and 8 all indicate that the fish comprising the second mode had a seasonal occurrence in the S.E. Cape and were most abundant from April to July.

Figure 7 shows that the occurrence of fish in Natal was also highly seasonal. In S. Natal they were most abundant from June to October and in N. Natal from July to November. It should be borne in mind that geelbek occurring in Natal were mostly larger than 900 mm FL.

These results therefore suggest that there is a seasonal movement of large A. aequidens (>900 mm FL) from the S.E. Cape to N. Natal.

Figure 6 indicated that the marginal increase in the catches of geelbek made during November and December in the S.E. Cape (see Figure 7) was a consequence of a concentration of smaller fish (<540 mm FL) which comprise the first mode of this regions bimodal length frequency distribution. Bearing in mind that there was a decrease from December to January in the general size

of the fish belonging to this mode, it was postulated that these fish concentrate to form shoals before migrating southwards to the S.W. Cape.

3.4 Conclusions

From the results and discussions presented in this chapter it may be concluded that A. aequidens off the South African eastern seaboard represent a single stock which is spatially divided into three age-related groups or sub-populations. These include: the 0 and 1 year olds which are found in the S.E. Cape and the S. Cape; the 1 to 4 year olds which occur in the S.W. Cape and the 4/5 to 9 year olds which undergo a seasonal migration from the S.E. Cape to Natal.

Although a considerable decline in the Natal catches occurred after October (Fig. 7) there is no evidence, in the catches from the respective regions, to suggest a return run. Catch analysis has also failed to reveal the whereabouts of the 1-4 year olds between March and December when catches in the S.W. Cape are observed to decline. In both cases the fish probably move beyond the limits of the linefishery.

In the subsequent chapters of this thesis the migration of the geelbek is discussed in relation to its biology and the physical oceanography of the South African east coast.

CHAPTER 4

AGE AND GROWTH

4.1 Introduction

The ability to determine the age of fish is an important tool in fisheries science. Age data in conjunction with length and weight measurements can provide information on stock composition, growth rate, age at maturity, mortality rates and the dynamics of fish migrations (Bagenal & Tesch 1978, Cushing 1981, Everhart & Youngs 1981). Much of this information is necessary for population assessments and the determination of optimal yields and hence is vital to fisheries management (Ricker 1975, Gulland 1983, Powers 1983, Pauly 1987, Summerfelt 1987).

The most frequently used method of age determination in fishes is the interpretation and counting of growth zones on their hard parts. Typical structures include scales, otoliths, vertebrae, fin rays and spines, cleithra and operculae (Nikolskii 1963, Bagenal & Tesch 1978, Everhart & Youngs 1981). After examining several of the above structures it was decided to use the otoliths for age determination in A. aequidens. Of the three otolith types present in the auditory bullae of teleost fish (Hecht 1978), the sagitta was chosen because it is much larger than either the astericus or the lapillus. Although scales have been most widely used in the past, recent validation and verification studies have shown that otoliths have a more distinct zonation, particularly in older fish, and consequently provide more accurate estimates of age (Casselman 1983, Carlander 1987, Beamish & McFarlane 1987). Studies on North American sciaenids have also indicated that otoliths provide the most accurate means of age determination for this group as a whole (Theiling & Loyacano 1976, Barger 1985, Maceina et al. 1987).

On the microscopic level otoliths are composed of calcium carbonate in the form of aragonite crystals which radiate

outwards in three dimensions from a central nucleus and pass through a matrix of fibrous protein called otolin (Degens et al. 1969, Morales 1986a, 1987). The calcium carbonate and the otolin are deposited differentially to produce alternate layers, or zones, of two optically and chemically distinct types. Due to the wide variety of techniques used for otolith preparation and viewing, there has been a considerable amount of confusion surrounding the terms used to describe these zones (Pannella 1974, Williams & Bedford 1974, Casselman 1983, Buxton & Clarke 1986, Hecht & Smale 1986, ICSEAF 1986, Buxton 1987). In the present study the term hyaline is used for those zones which transmit light and the term opaque for those which do not. Chemically hyaline zones contain more calcium than opaque zones which have a higher otolin content (Dannevig 1956, Irie 1960, Mugiya 1965, Casselman 1974, Morales 1986b). Adjacent hyaline and opaque zones which represent a year's growth are collectively referred to as an annual growth zone or annulus.

Growth models are usually fitted to age data because they provide a generalized description of growth which may be used for comparative purposes or more importantly for stock assessment and fisheries management (Gulland 1983). The von Bertalanffy growth (VBG) equation, which is the most widely used model for expressing fish growth (Allen 1966, Hecht 1976, Schnute 1981, Brothers 1983, Moreau 1987), was fitted to the age and size data for A. aequidens. Additional advantages of the VBG equation are that certain of its parameters may be directly incorporated into stock assessment models (Beverton & Holt 1957, Ricker 1975, Vaughan & Kanciruck 1982) or used for estimates of natural mortality (Pauly 1980).

4.2 Material and Methods

Otolith Preparation and Reading

Due to the thickness and overall opacity of geelbek otoliths, it was necessary to section all otoliths. Sections along the line

of maximum growth (longitudinally) produced the best results. Burning (Christensen 1964, Buxton 1987), before or after sectioning, did not improve readability.

Although a total of 1100 otolith pairs were collected during the course of this study, only 580 were used for growth analysis. To avoid errors due to an inadequate data range (Hirschhorn 1974, Hughes 1986) the otoliths were selected so that all sizes within the range of fish sampled (250-1055 mm FL), were represented. Of the chosen otoliths, 207 were collected during 1985 and 353 during 1986.

One otolith from each pair was embedded in a clear casting resin rod and sectioned (0,5 mm) using a double-bladed, diamond edged saw similar to that described by Rauck (1976). Care was taken to ensure that the sections were cut through the nuclei of the otoliths. Each section was mounted on a glass slide and viewed against a black background under reflected light using a dissecting microscope (Fig. 9). Distinct growth zones were observed which appeared very similar to those of other sectioned sciaenid otoliths, e.g. A. hololepidotus (Wallace & Schleyer 1979), the Atlantic croaker, Micropogonias undulatus (Barger 1985), the red drum Sciaenops ocellatus (Theiling & Loyacano 1976) and the spotted seatrout Cynoscion nebulosus (Maceina et al. 1987).

The otoliths were initially read once to gain familiarity with ring pattern. They were then read a further three times, at least one week apart and without any reference to size, locality or time of collection, to record the number of opaque and hyaline zones. Only those counts occurring at least twice for each otolith were accepted. As a consequence 20 otoliths (3,4%) of the total sample had to be rejected.

In order for otoliths to be used for ageing purposes, it is necessary to determine the number of growth zones deposited in a year. To this end the percentage of opaque and hyaline margins



Figure 9. A sectioned otolith from a five year old geelbek, viewed under reflected light. N = nucleus.

were calculated for the otoliths on a monthly basis.

Growth Calculations

Student t tests on the mean length at age data ($P < 0,05$) and a "Likelihood Ratio Test" on all data points showed no significant differences between the growth rates of the males and the females. The data for the two sexes were therefore combined for the purpose of growth calculations and for the construction of an age length key.

The von Bertalanffy (1934, 1938, in Ricker 1975) growth model in the form of:

$$L_t = L_{\infty} [1 - e^{-k(t-t_0)}]$$

where L_t = length at age t
 L_{∞} = theoretical asymptotic length
K = growth coefficient
 t_0 = theoretical age at zero length

was fitted to the fork length-at-age data. Until recently Beverton's (1954) method, involving unweighted mean lengths-at-age and the use of a Ford Walford plot, was the most frequently used for this purpose (Moreau 1987). However, by using mean length-at-age data equal weight is given to each age point and, therefore, unrealistically assumes that sampling error is zero (Schnute 1981, Hughes 1986). As shown by Hughes (op. cit.) the application of more advanced curve fitting techniques can yield totally different results.

Because of the above, attempts were made to fit the von Bertalanffy equation using the absolute error and the transformed logarithmic error models described by Hughes (1986). Both of these methods include all length-at-age values. Unfortunately, the results did not pass the error model tests for homoscedacity and randomness, which meant that the VBG parameters could not be

accepted with any degree of confidence (Hughes 1986). This has been attributed to the paucity of fish represented in the older year classes (G. Hughes & A. Punt, Department of Applied Mathematics, University of Cape Town, pers. comm.). In view of the above the VBG equation derived using Beverton's method was used for all growth related calculations.

Although it was possible to consistently section through the otolith nucleus, the exact angle and plane of sectioning (due to the position of the otolith within the resin rod) could not be precisely maintained. As pointed out by Williams and Bedford (1974), although a fractional difference in the point at which a section is made may be perfectly acceptable for age determination, a considerable difference in the size of the rings that are visible for measurement might occur. For this reason back-calculations, which rely on the relationship between annulus radius and fish length, were not attempted.

For stock assessment and yield optimization, it is often required that growth be expressed in terms of weight (Ricker 1975, Dickie 1978, Pitcher & Hart 1982, Gulland 1983, see also Chapter 7). For this purpose the VBG model may be rewritten as:

$$W_t = W_{\infty} [1 - e^{-k(t-t_0)}]^b$$

where W_t is weight at age, W_{∞} is the asymptotic weight and b is the exponential value from the length-weight relationship. W was determined by substituting L_{∞} into the length-weight equation.

The relationship between length and weight in fish takes the form of:

$$W = aL^b$$

where W is weight, L is length and a and b are constants (Bagenal & Tesch 1978, Gulland 1983).

A logarithmic transformation of this equation gives:

$$\text{Log } W = \log a + b \log L$$

The length/weight relationship for the geelbek was therefore calculated by plotting a least squares linear regression of log FL (mm) against log weight (g) where a = abscissa intercept and b = the slope.

Legal size limits for the South African linefishery are expressed in terms of total length except, in Natal where FL is used. It was therefore necessary to calculate, by a least squares regression, the fork length/total length relationship, so that lengths-at-age could be expressed in terms of total length for management recommendations.

4.3 Results

The otoliths of A. aequidens exhibit wide opaque and narrow hyaline zones (Fig. 9). Figure 10 showing the percentage monthly opaque and hyaline margins, revealed that as in the case of other sciaenids (Theiling & Loyacano 1976, Wallace & Schleyer 1979, Barger 1985, Maceina et al. 1987, T. Hecht, Department of Ichthyology and Fisheries Science, Rhodes University, pers. comm.) one hyaline and one opaque zone were deposited per year and therefore comprised an annulus.

The age length key for A. aequidens is presented in Table 3.

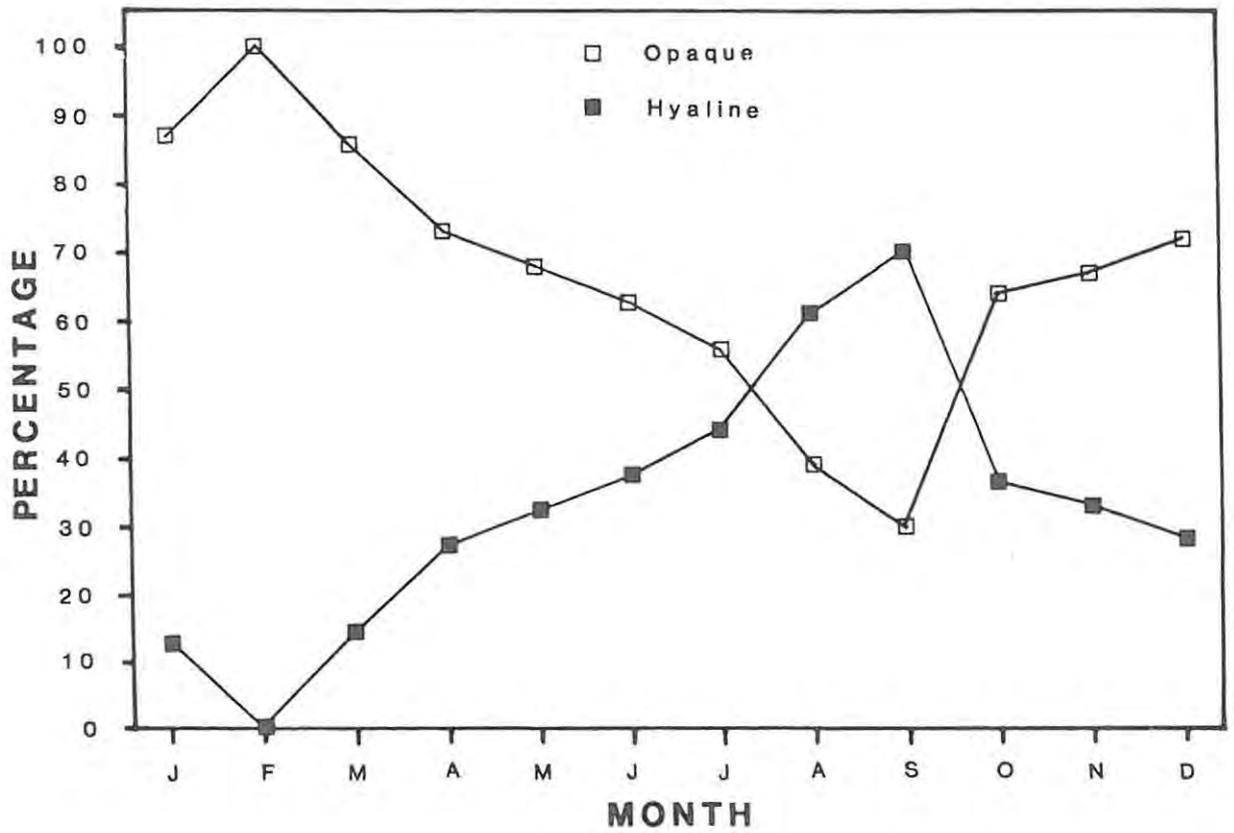


Figure 10. The monthly percentage of opaque and hyaline otolith margins from fish sampled along the South African east coast from 1985 to 1987 (n = 580).

Table 3. Age/Length key for Atractoscion aequidens on the South African east coast(1985/86).

Fork Length (mm)	Age (years)										All Ages	
	0	1	2	3	4	5	6	7	8	9		
270-299	1											1
300-329	5											5
330-359	15											15
360-389	19											19
390-419	19	2										21
420-449	20	10										30
450-479	8	9										17
480-509	3	9										12
510-539	1	16	1									18
540-569		15	4									19
570-599		9	6									15
600-629		6	10									16
630-659		3	16	3								22
660-689			22	2								24
690-719			16	6								22
720-749			12	6	1							19
750-779			10	9	1							20
780-809			3	8	3	1						15
810-839				11	3	1						15
840-869				5	18	3						26
870-899					20	5	1					26
900-929					18	12	2					32
930-959					11	30	3	1				45
960-989					2	13	13	4				32
990-1019						10	15	8	2			35
1020-1049						3	8	7	10	2		30
1050-1080							2	4	3			9
All Lengths	91	79	100	50	77	78	44	24	15	2		560

The VBG equations calculated by the three different fitting procedures are presented in Table 4 and illustrated in Figure 11.

Table 4. The von Bertalanffy growth equations for Atractoscion aequidens derived using the absolute error model, the transformed logarithmic error model and Beverton's mean length-at-age method.

METHOD	EQUATION
Beverton (1954)	$L_t = 1104 [1 - e^{-0,25(t+1,64)}]$
Absolute error (Hughes 1986)	$L_t = 1173 [1 - e^{-0,23(t+1,53)}]$
Transformed logarithmic error (Hughes 1986)	$L_t = 1272 [1 - e^{-0,19(t+1,76)}]$

Figure 12 depicts the VBG relationship derived using Beverton's method together with the mean observed lengths-at-age.

No significant difference ($P < 0,05$) was found between the length/weight data of male and female geelbek. The length/weight relationship was therefore calculated from a combined data set and is described by the equation:

$$W_{(g)} = 8,42 \times 10^{-6} FL^{3,01}(\text{mm}) \quad n = 1200, r^2 = 0,994$$

A b value (3,01) which was essentially equal to three indicates that this species displays isometric growth (Ricker 1975) and that body form does not change significantly over the length range (270 mm - 1065 mm FL) used for the above calculation.

The growth of A. aequidens expressed in terms of weight could therefore be described by the equation:

$$W_t = 12152 [1 - e^{-0,25(t+1,64)}]^{3,01} \quad (\text{Figure 13})$$

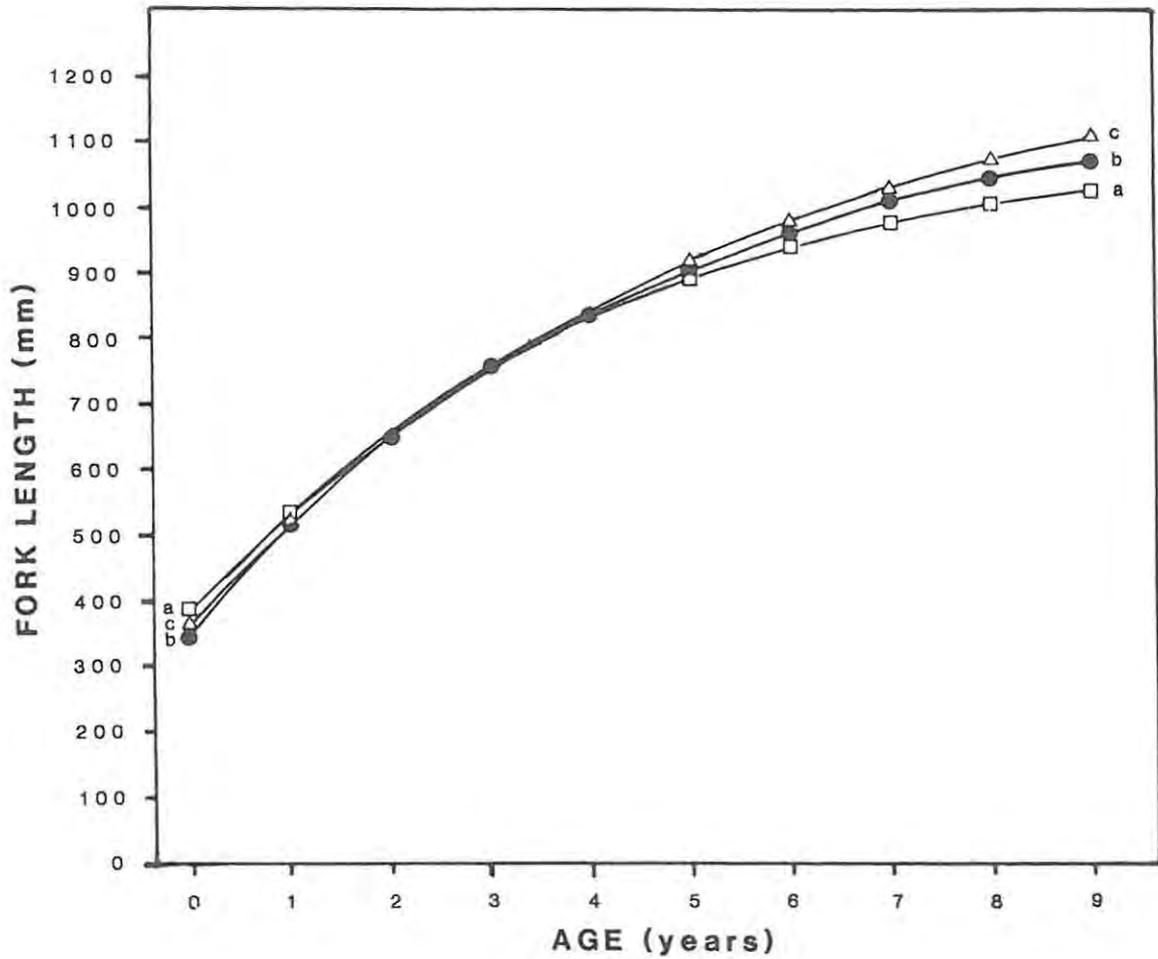


Figure 11. Three curves, derived by fitting the von Bertalanffy growth model to the length-at-age data for Atractoscion aequidens using a) Beverton's mean length-at-age method, b) the absolute error model and c) the transformed logarithmic error model.

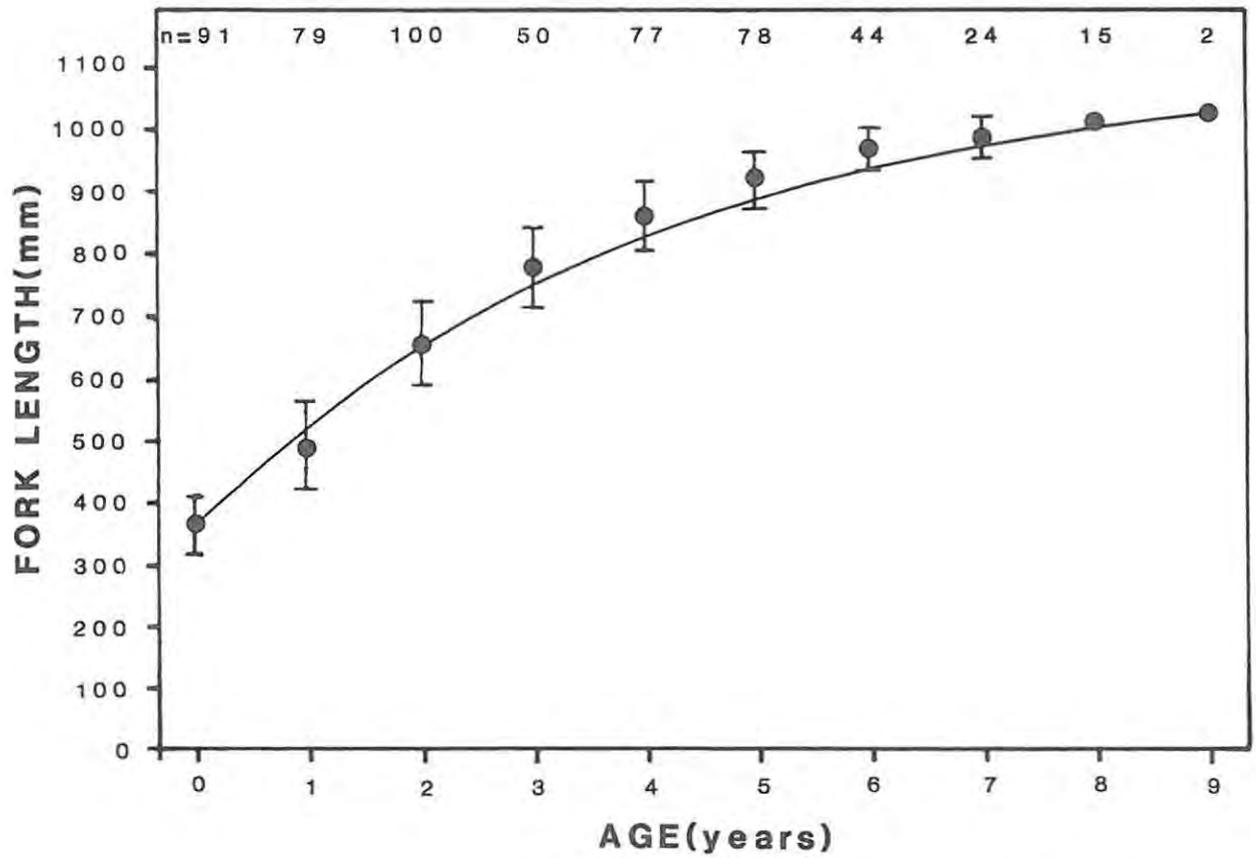


Figure 12. Observed and calculated length-at-age data for *Atractoscion aequidens* sampled along the South African eastern seaboard during 1985 and 1986. The n values give the number of fish sampled from each age group.

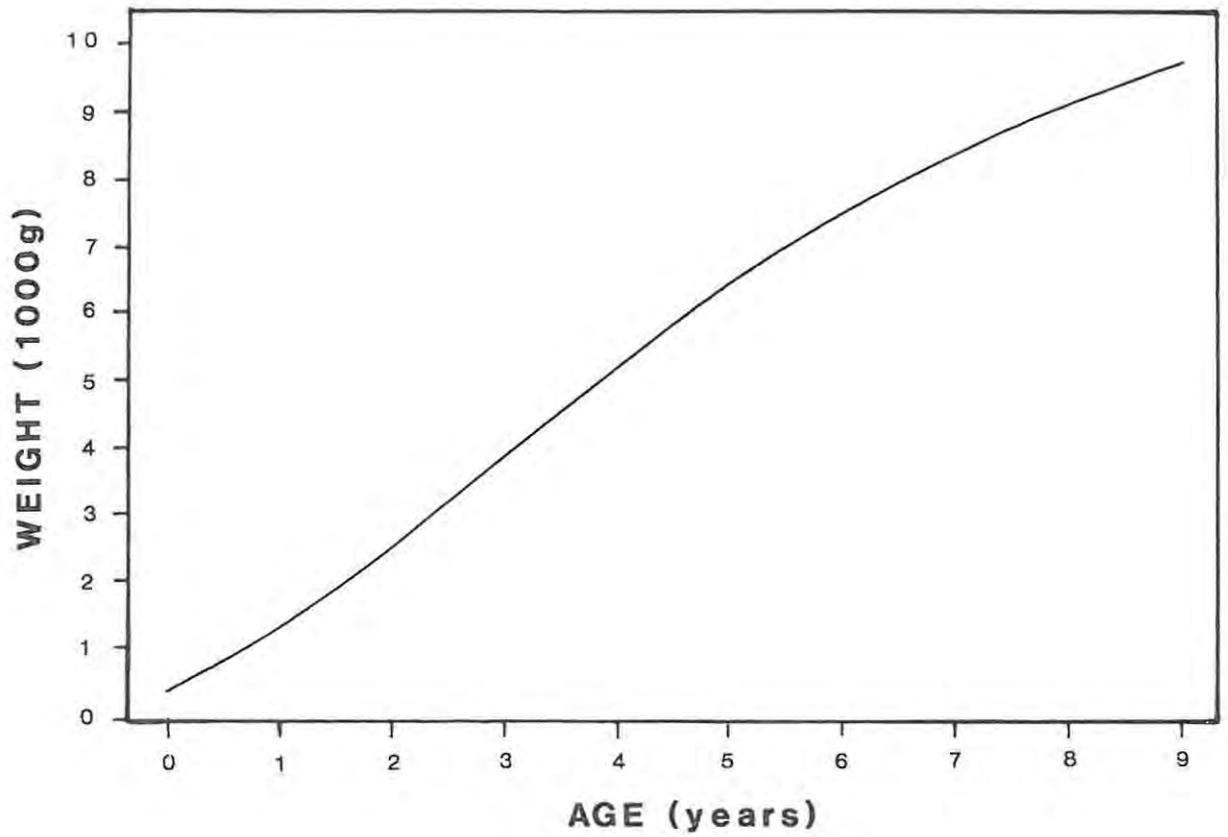


Figure 13. Calculated growth in terms of weight for Atractoscion aequidens along the South African eastern seaboard.

The fork length/total length relationship was described by the equation:

$$TL = 1,06 FL - 0,757$$

$$n = 500, r^2 = 0,997,$$

Data range = 270-1065 mm FL

4.4 Discussion

Figure 11 shows that the curves described by all three relationships in Table 4 were very similar for the first five years of growth, but began to deviate from each other after this point. It is relevant to mention here that even though a concerted effort was made to sample fish from the older year classes great difficulty was encountered in obtaining fish above six years of age. This implies that these fish make very low contributions to the biomass and growth of the geelbek population as a whole. Consequently slightly inaccurate estimates of the growth rate for the older age groups should not seriously impair stock assessments based on the VBG parameters.

Casselman (1983) showed that growth data (particularly L_{∞}) obtained from age assessments should be credible when compared with observed measurements. As explained by Ricker (1975), L_{∞} is the asymptotic length to which the average uncaptured fish in a population would grow and is not intended to represent those of record size. Therefore, considering that the largest fish measured during the present study was 1065 mm FL, and that the largest geelbek ever recorded was 1300 mm TL, 1227 mm FL (Heemstra 1986), the L_{∞} value of 1104 mm FL obtained using Beverton's (1954) method (see Table 4) was considered to be realistic.

Stimulated largely by the discovery that scales have provided gross underestimates of age for many species, numerous authors have stressed the importance of validating age determinations (Beamish & McFarlane 1983, Casselman 1983, Carlander 1987). Although the monthly analysis of otolith margins, may be regarded

as an indirect technique for age validation (Brothers 1983, Hecht & Smale 1986), additional validation was achieved for the first four years by analysing length frequencies. Figure 14 which graphically illustrates the annual percentage length frequencies of fish sampled in the S.W. Cape (from Table 2), clearly shows that the geelbek in this region had a trimodal length frequency distribution. The first mode peaked between 510 and 570 mm and corresponds with the 533 mm FL calculated by the VBG equation for one year old fish. The second modal peak lay between 660 and 720 mm. This was considered to be the result of an overlap of the length distributions of the two and three year old fish which have calculated lengths of 655 mm and 758 mm FL respectively. For some unknown reason this mode was completely missing from the 1985 length measurements. The third modal peak of the S.W. Cape length frequency distribution occurred at the 810-840 mm size class. The calculated length-at-age for four year old fish was 834 mm. Due to the migratory nature of the larger geelbek (>4 years) and the length frequency overlap which is generally associated with older age groups (Bagenal & Tesch 1978), this method was not suitable for fish older than four years. The use of more comprehensive validation techniques (see Casselman 1983, Brothers 1983, Beamish & McFarlane 1987) such as mark-recapture studies and fluorochrome labels e.g. oxytetracycline, were beyond the scope of this project.

A comparison of Figures 10 and 28 indicated that hyaline accretion, which reached a peak in spring, was directly related to gonad maturation. Hyaline zone formation in several sciaenid species occurring off West Africa and Puerto Rico have also been linked with spawning activity (Pannella 1974). Because of the protein and energetic requirements for gonad development, a decrease in skeletal and somatic growth during such periods would be expected (Casselman 1974, Calow 1985). In addition, hyaline accretion occurred during the period when the energy reserves of sexually immature fish are at their lowest (see Chapter 6). It was therefore tempting to suggest that hyaline zone formation is associated with periods of slow growth, and opaque zones with

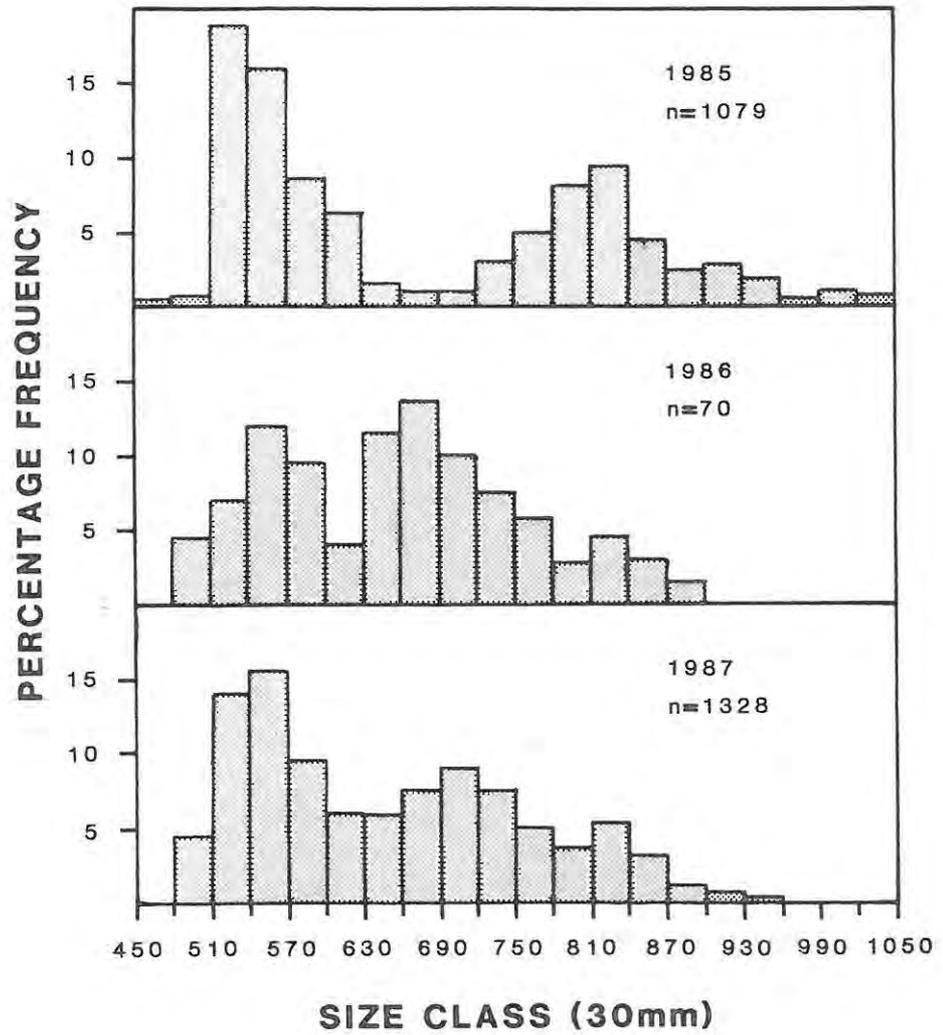


Figure 14. Annual fork length frequency distributions of Atractoscion aequidens from the South West Cape, 1985-1987.

periods of fast growth. This conclusion would be consistent with the general theory on this topic (Pannella 1971, 1974, Williams & Bedford 1974, Bagenal & Tesch 1978, Hecht & Smale 1986, ICSEAF 1986).

In the South African context Botha (1971) has shown that hyaline zone deposition in the Cape hakes (Merluccius capensis and Merluccius paradoxus) is associated with the spawning period. Numerous other authors in this country have also concluded that hyaline zones are formed during periods of slow somatic growth (Geldenhuis 1973, 1978, Nepgen 1977, Hecht 1976, Hecht & Baird 1977, Coetzee & Baird 1981, Thomas 1983, 1985, Buxton & Clarke 1986). However, Buxton (1987) has questioned these conclusions and postulated that in many of these studies hyaline zones were in fact representative of fast growth. He has also correlated hyaline zone accretion with rapid somatic growth in two sparid species, viz. Chrysoblephus laticeps and C. cristiceps. Similar conclusions have also been reached by several authors working on various species in the northern hemisphere (e.g. Molander 1947, Dannevig 1956, Irie 1960).

Although it has been established that seasonal changes occur in the quantitative and qualitative growth of otoliths, the physiology of these processes remain unclear. Because otolith growth occurs as a result of the differential deposition of calcium carbonate and protein, the metabolism of either or both of these two components is believed to be central to annulus formation (Mugiya 1966, Irie et al. 1967, Casselman 1974, Simkiss 1974). It therefore follows that any factor which affects protein and or calcium metabolism may influence otolith growth. Examples of factors which have been implicated in annulus formation include photoperiod (Mugiya et al. 1981), water temperature (Dannevig 1956, Thomas 1983, Melo 1984) food availability (Trout 1958, in Casselman 1974, Bilton 1974, Ortega-Salas 1980) and reproductive condition (Hickling 1933, Bruton & Allanson 1974, Botha 1971, Hecht 1976, Griffiths & Hecht 1986).

Graham (1929, in Williams & Bedford 1974) postulated that endogenous rhythms also play an important role in annulus formation. Subsequent studies on the microstructural growth of otoliths (Campana & Nielsen 1985, Beamish & McFarlane 1987), work on fish maintained in uniform environments (Brown 1946, Williams & Bedford 1974), and by several authors who have presented evidence to show that zone deposition in immature fish is inherently linked to the reproductive cycle (Hickling 1935, Botha 1971, Geldenhuys 1973, Hecht 1976), all support this theory.

At this stage it would be impossible to disentangle the effects of endogenous rhythms and the various environmental and reproductive conditions in order to assess the relevance of each to the formation of annuli on the otoliths of different species. It is, however, evident that the physiological changes which influence otolith growth would not necessarily also affect somatic growth rate. A better understanding of otolith growth, in respective species, might therefore be obtained by attempting to relate zone formation to environmental or physiological conditions, regardless of their effect on the somatic growth. In the case of the geelbek it is most probable that physiological changes associated with gonad maturation in mature fish are responsible for hyaline accretion, and that as in the case of other species, zone formation in immature fish is linked to the reproductive cycle by means of an endogenous rhythm.

CHAPTER 5

ASPECTS OF THE REPRODUCTIVE BIOLOGY

5.1 Introduction

The success of any fish species is ultimately determined by the ability of its members to reproduce successfully in a fluctuating environment and thereby to maintain viable populations (Moyle & Cech 1982). Fishes exhibit a diverse range of reproductive strategies involving elaborate behavioural, anatomical and physiological adaptations to maximize reproductive success (Breder & Rosen 1966, Nikolskii 1963, Balon 1975).

Although studies on reproduction contribute to the overall understanding of the biology of a species, such studies are also important for its management. Relevant aspects include the determination of the age and size at sexual maturity, the breeding season and the spawning area. These aspects are also important for understanding and explaining fish migrations (Harden-Jones 1968).

Due to their commercial and recreational importance the reproductive biology of sciaenids on the east and west coasts of North America have received much attention (inter alia Tabb 1961, Moffet 1961, Breder & Rosen 1966, Johnson 1978, Moffet et al. 1979, Vojkovich & Reed 1983, Ross 1984, Shepherd & Grimes 1984). Conspicuous features of sciaenid reproductive biology are their small pelagic eggs and specialized sonorific muscles in the males of most species. These muscles are apparently used for sound production during spawning (Breder & Rosen 1966, Adler 1975, Johnson 1978, Holt et al. 1985, Mok & Gilmore 1983).

Of the nine species of sciaenids that occur along the South African coast (Heemstra 1986) eight are commonly caught by line and spearfishermen. Three of these form important components of the commercial and recreational linefishery (Van der Elst 1981,

Heemstra 1986). The kob (Argyrosomus hololepidotus) is the only South African species on which fairly comprehensive reproductive data have been published (Smale 1985).

The reproductive biology of A. aequidens is presently poorly understood. Based on somewhat sparse information obtained chiefly from Algoa Bay, Smale (op. cit.) speculated that the size at first maturity for males occurred at a fork length of ± 590 mm and for females at ± 650 mm. He also suggested that spawning takes place between May and July, either in water deeper than that fished by fishermen, or along the eastern Cape coast outside his specific study area. Van der Elst (1981) observed reproductively "ripe" geelbek in Natal during the winter months and postulated that these fish migrate northwards in order to spawn in the warmer waters off the Natal coast.

The aim of the present investigation was to establish the spawning season and the spawning grounds of the geelbek and to determine the age and size at sexual maturity. The precise timing and location of spawning in teleost fishes are adaptations which ensure optimal conditions (biotic and abiotic) for the survival of progeny (Bond 1979, Crim 1982, McKeown 1984). In many species these adaptations include extensive seasonal spawning migrations (Harden-Jones 1968, Nikolskii 1963, Cushing 1981, McKeown op. cit.). The length and age at sexual maturity are basic criteria for fisheries management. They may be used for the formulation of size limits (Nikolskii 1969, Cushing 1981), the calculation of rates of natural mortality (Rikhter & Efanov 1977) and for spawner biomass per recruit models (see Chapter 7). These two aspects of reproductive biology also contribute to the general understanding of the reproductive strategy of a species (Balon 1975, Stearns 1976). The sex ratio of the South African geelbek population was also investigated.

Because the primary objectives of this study amounted to an investigation of the dynamics and the temporal and spatial patterns of the hypothetical migration of this species, it was

decided not to undertake a microscopic examination of gonadal development. Fecundity studies were also omitted.

5.2 Materials and Methods

Reproductive Seasonality and Spawning Areas

The most widely used methods to establish the breeding season of fishes and their spawning locality are those based on indices of gonad maturity which are derived from either visual descriptions or calculations involving gonad weight (e.g. Hecht 1976, Elder 1976, Van der Elst 1976, Garrat 1984, Shepherd & Grimes 1984). As mentioned in Chapter 2 the gonads of all biologically sampled geelbek were weighed and assigned an index of visual maturity.

To avoid a possible masking effect which could be introduced through using data from immature fish, usually only those data from fish above the size at 100% sexual maturity are used to determine reproductive seasonality and spawning area (Hecht 1976). However, as a result of the migratory nature of the geelbek, it was discovered that most fish found in the S.E. Cape and Natal, which were above 900 mm FL, the size at 50% maturity, were sexually active (see section 5.3). Consequently data pertaining to the gonads of geelbek above 900 mm FL were used to determine the reproductive seasonality and spawning locality of this species.

The gonads of A. aequidens are elongate paired structures of equal size which extend throughout the entire length of the abdominal cavity. They are attached along their entire length to the lower left and right walls of the swimbladder by delicate mesenteries. Descriptions of each maturity stage are given in Table 5.

Table 5. Classification of the macroscopic gonad maturity stages of A. aequidens

STAGE	DESCRIPTION
I. Juvenile	This stage is generally only found in fish below 320 mm FL. Gonads appear as transparent thread-like structures which are unsexable.
II. Immature or Resting (Figs. 15 & 16)	Testes are extremely thin, flat and pinkish white in colour. Ovaries appear as translucent orange tubes. Eggs are not visible to the naked eye.
III. Active (Figs. 17 & 18)	Testes are wider, triangular in cross-section and beige in colour. Sperm is present if cut and gently squeezed. In the females, eggs become visible to the naked eye as tiny yellow granules in a gelatinous orange matrix. There is very little increase in the diameter of the ovary.
IV. Developing (Figs. 19 & 20)	Testes become wider, deeper and are a mottled creamy beige in colour. They are also softer in texture, rupturing when lightly pinched. Besides the obvious presence of sperm in the main sperm duct, some sperm is also present in the tissue. Ovaries become larger in diameter and opaque yellow in colour. Clearly discernible eggs occupy the entire ovary.
V. Ripe (Figs. 21 & 22)	Testes still larger in cross-section and softer in texture. They become creamier in colour due to considerable quantities of sperm within the tissue. The ovaries are larger in diameter as a result of an increase in egg size.
VI. Ripe/Running (Fig. 23)	The gonads are even larger in cross-section. They are extremely delicate at this stage and break up easily when handled. The testes are uniformly cream in colour and the ovaries are amber. Most of the

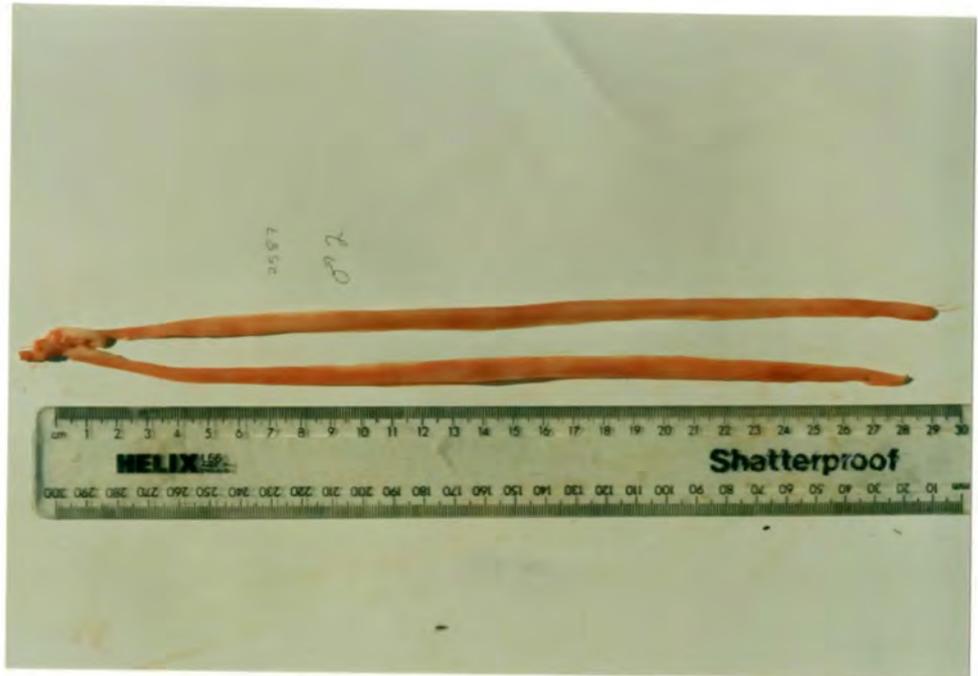


Figure 15. Stage II testes of Atractoscion aequidens. Fat removed.



Figure 16. Stage II ovary of Atractoscion aequidens.

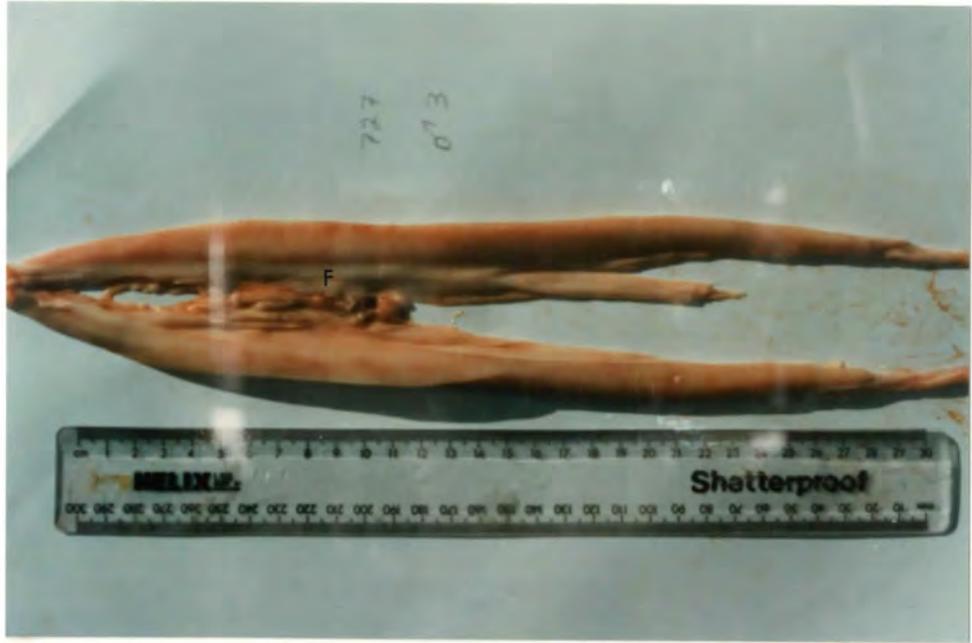


Figure 17. Stage III testes of *Atractoscion aequidens*. Note the fat (F) associated with the gonad.



Figure 18. Stage III ovary of *Atractoscion aequidens*.

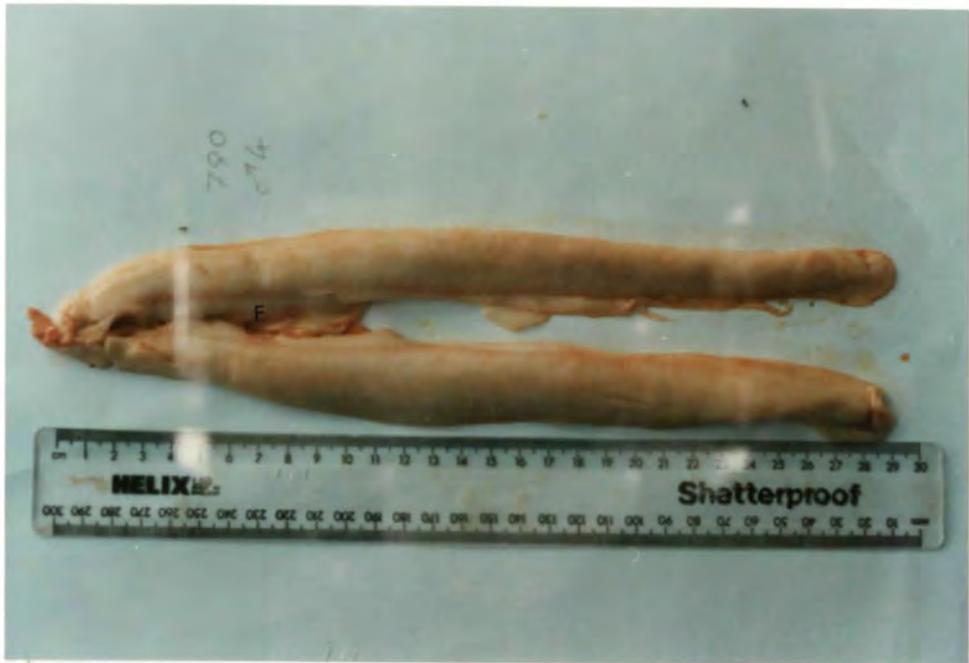


Figure 19. Stage IV testes of Atractoscion aequidens. Fat (F) partly removed.



Figure 20. Stage IV ovary of Atractoscion aequidens. Note the large quantity of fat (F) attached to the gonad.

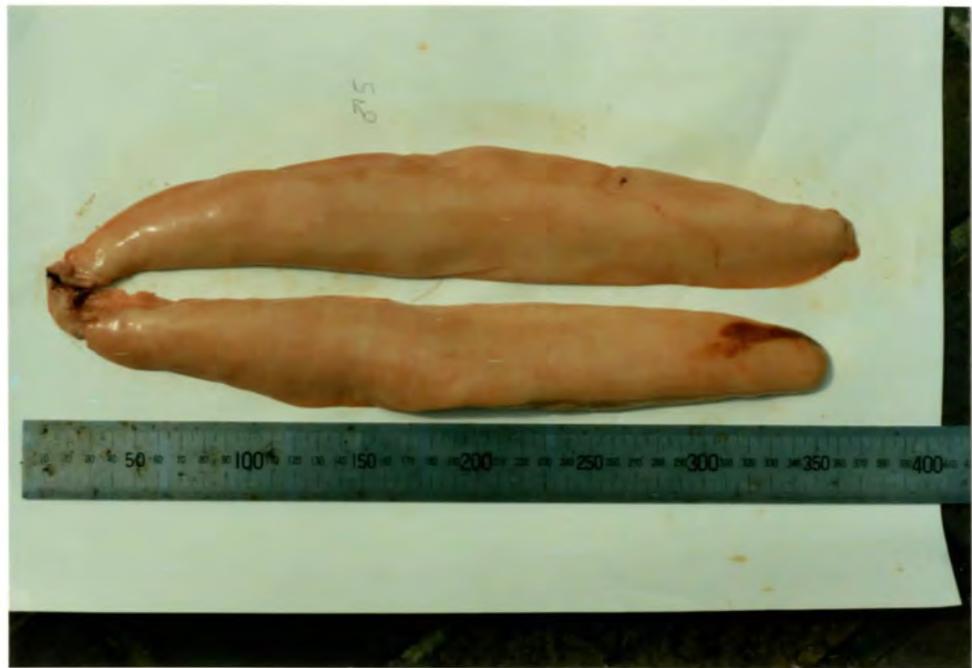


Figure 21. Stage V testes of Atractoscion aequidens.



Figure 22. Stage V ovary of Atractoscion aequidens. F = fat.

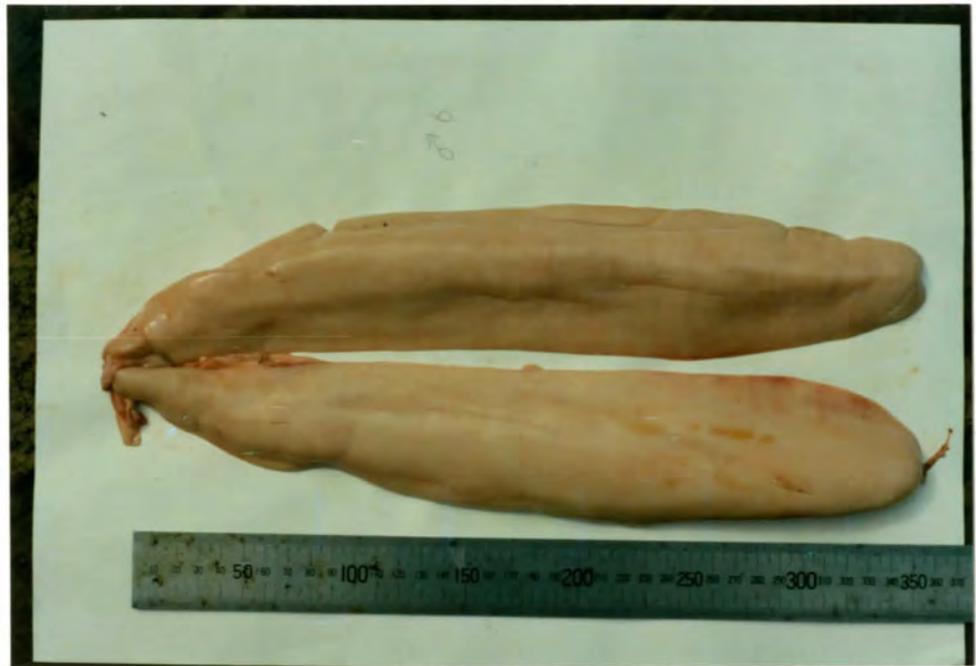


Figure 23. Stage VI testes of Atractoscion aequidens.

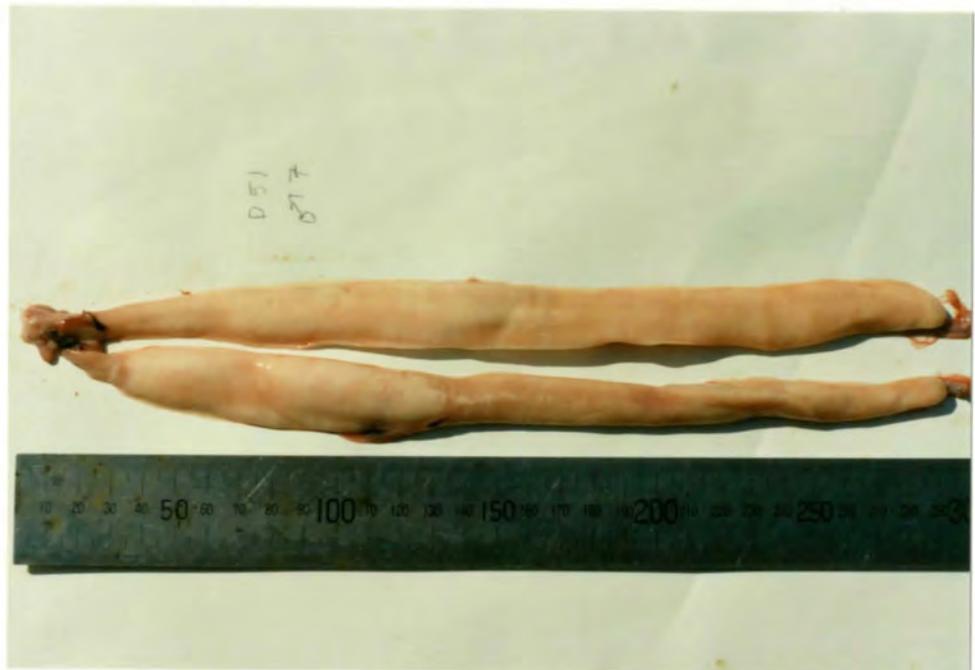


Figure 24. Stage VII testes of Atractoscion aequidens.

eggs are large ($\pm 1,2\text{mm}$) and transparent. Eggs and sperm are freely extruded when pressure is applied to the abdomen of whole fish.

VII. Spent
(Fig. 24)

Testes are shrivelled in appearance and a mottled beige and cream in colour. A little viscous semen may ooze from the genital pore when pressure is applied to the abdomen. No spent ovaries were observed.

Monthly percentage frequencies of each maturity stage were calculated for both males and females examined in three of the study regions (S.W. Cape, S.E. Cape and S. Natal).

A Gonadosomatic Index (GSI), as first introduced by Meien (1927, in Delahunty & de Vlammig 1980) was calculated as follows:

$$\text{GSI} = (\text{Gonad weight/Fish Weight}) \times 100$$

According to Shul'man (1974, in de Vlammig *et al.* 1978) fat supplies the major source of energy for gamete production in fishes. A Somatic Fat Index (SFI) was therefore computed by substituting visceral fat weight for gonad weight in the above equation.

Mean monthly Gonadosomatic and Somatic Fat indices were calculated for fish sampled in each region in order to establish the seasonal trends in gonad development and fat accumulation, and also to determine how these were related.

Length and Age at Sexual Maturity

The size at 50% sexual maturity is usually determined by calculating the percentages of mature and immature gonads observed for fish of given size classes during the breeding season (e.g. Hecht 1976, Van der Elst 1976, Elder 1976, Botha 1986, Standard & Chittenden 1984, Garrat 1984, Buxton 1987). This method was however unsuitable for A. aequidens as all fish

in the breeding area were mature. An alternative method was therefore developed.

Based on the rationale that the geelbek migrate to Natal to breed (see section 5.3), it would be logical to assume that the most highly represented size class in the migratory portion of the population, would be 100% sexually mature. It then theoretically follows that the length at 50% maturity would correspond with a lower size class having half that representation. Lower representation in size classes above the size at 100% maturity would obviously be due to mortality rates. Percentage length frequencies were calculated separately for the males and females of the migratory portion of the stock in the S.E. Cape, and also for those that reached Natal. To ensure that data from the mature migratory portion of the geelbek population were used for these calculations, only those lengths from fish with gonads in stage III or above were considered.

A transformation of the von Bertalanffy growth equation (see Chapter 4) was used to convert length-at-maturity to age-at-maturity.

Sex Ratios

To enable a more thorough analysis of the sex ratio of the South African geelbek population, the fish sampled in the S.W. and S.E. Cape were divided into 250 mm length classes. Sex ratios were computed for each size class and also for the regional totals. Because of the relatively low numbers of fish sampled in Natal and the fact that most of them belonged to the 750-1000 mm size class (see Chapter 3), a sex ratio was only calculated for the total sample.

Chi-square analyses were performed to ascertain whether the observed ratios deviated significantly from unity.

5.3 Results and Discussion

Reproductive Seasonality and Spawning Areas

Figures 25 to 27 illustrate the monthly percentage frequencies of the various visually determined gonad maturity stages. Mean monthly GSI's are shown in Figure 28.

In Chapter 3 it was shown that geelbek larger than 900 mm FL were present in the S.E. Cape from April to August. Figures 26 & 28 show that there was a progressive development of both male and female gonads in the S.E. Cape during this period. However, it should be noted that the spawning condition (Stage VI) was not recorded in this region. Figures 26 to 28 also show that the gonads collected in southern Natal during September and October were generally in a more advanced stage of development than those collected in the S.E. Cape during July and August. The occurrence of a substantial percentage of ripe running male and female fish in southern Natal and the absence of fish in this stage of gonadal maturity in the S.E. Cape would indicate that spawning occurs off the Natal coast.

Because detailed biological data were only collected in Natal during the months of September and October, these results alone were insufficient upon which to draw a firm conclusion on the temporal extent of the breeding season. Unpublished gonad indices calculated by Denton (ORI, Durban, pers. comm.) from data collected in Natal during 1985 and 1986, and made available for analysis, however, indicate that peak spawning occurs in September and October. Furthermore, the gonads of fish examined in Natal by Garrat (ORI, pers. comm.) during late August of 1984 were also found to be ripe. It therefore becomes apparent that although geelbek first arrive in southern Natal in June (Chapter 3) maximum spawning activity only occurs from August to October. On completion of spawning the fish leave this region. Similar observations have been made for the elf Pomatomus saltatrix (Van der Elst et al. 1978) and the leervis Lichia amia (Van der Elst

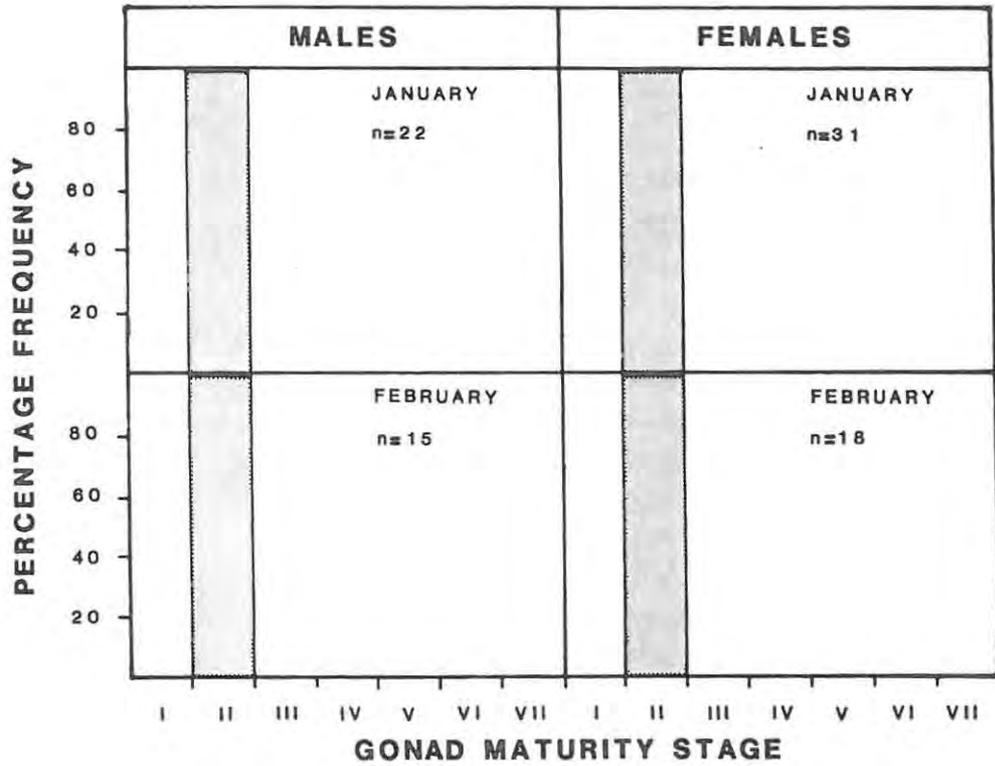


Figure 25. Percentage frequency of the visual gonad maturity stages observed for Atractoscion aequidens (>900 mm FL) in the South West Cape.

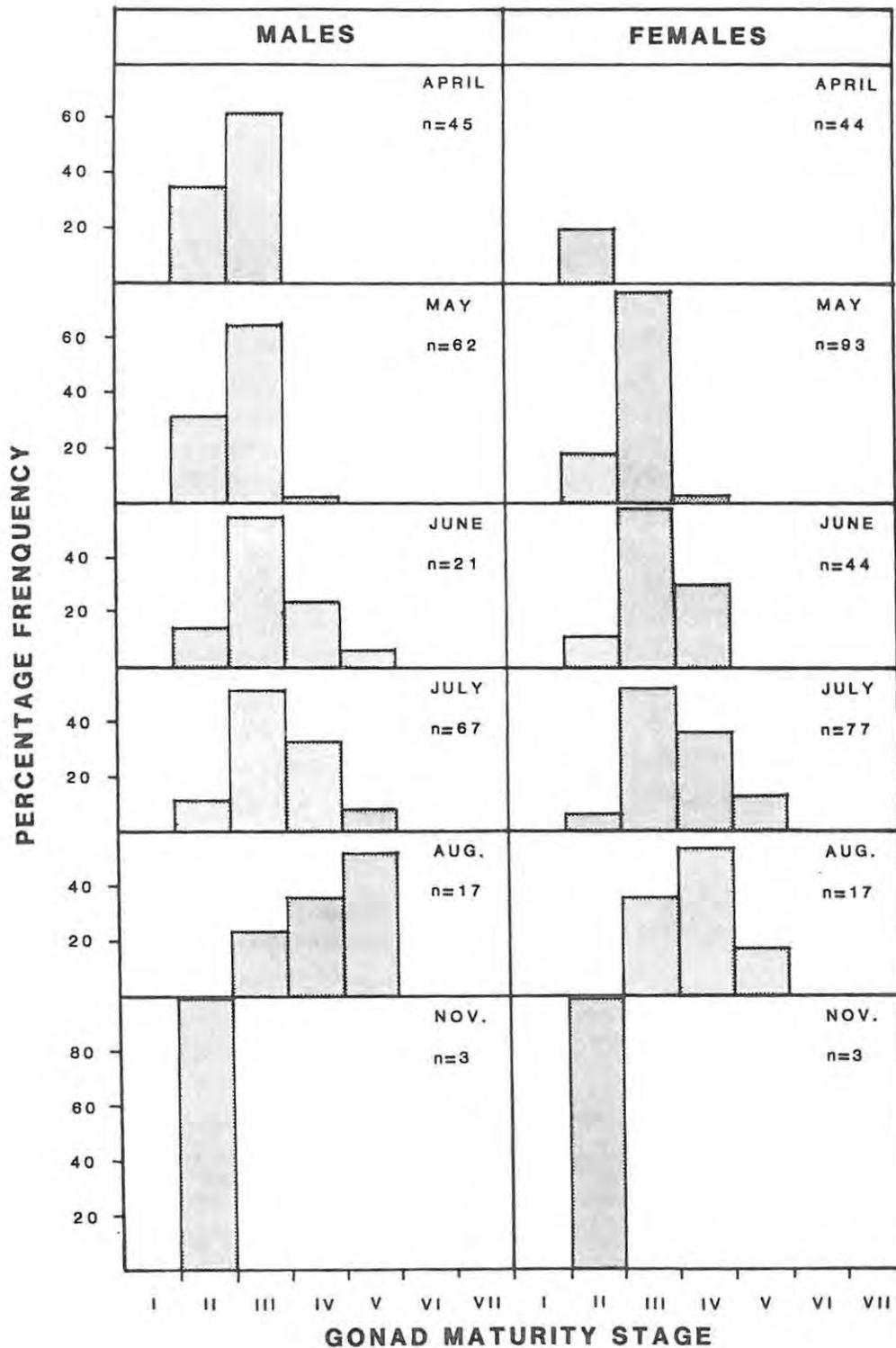


Figure 26. Percentage frequency of the visual gonad maturity stages observed for *Atractoscion aequidens* (>900 mm FL) in the South East Cape.

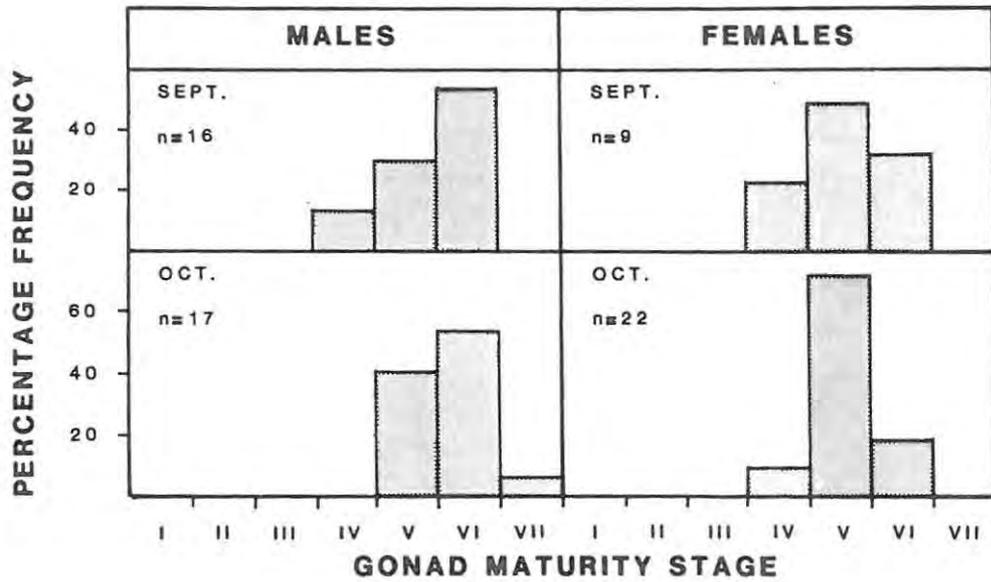


Figure 27. Percentage frequency of the visual gonad maturity stages observed for *Atractoscion aequidens* (>900 mm FL) in South Natal.

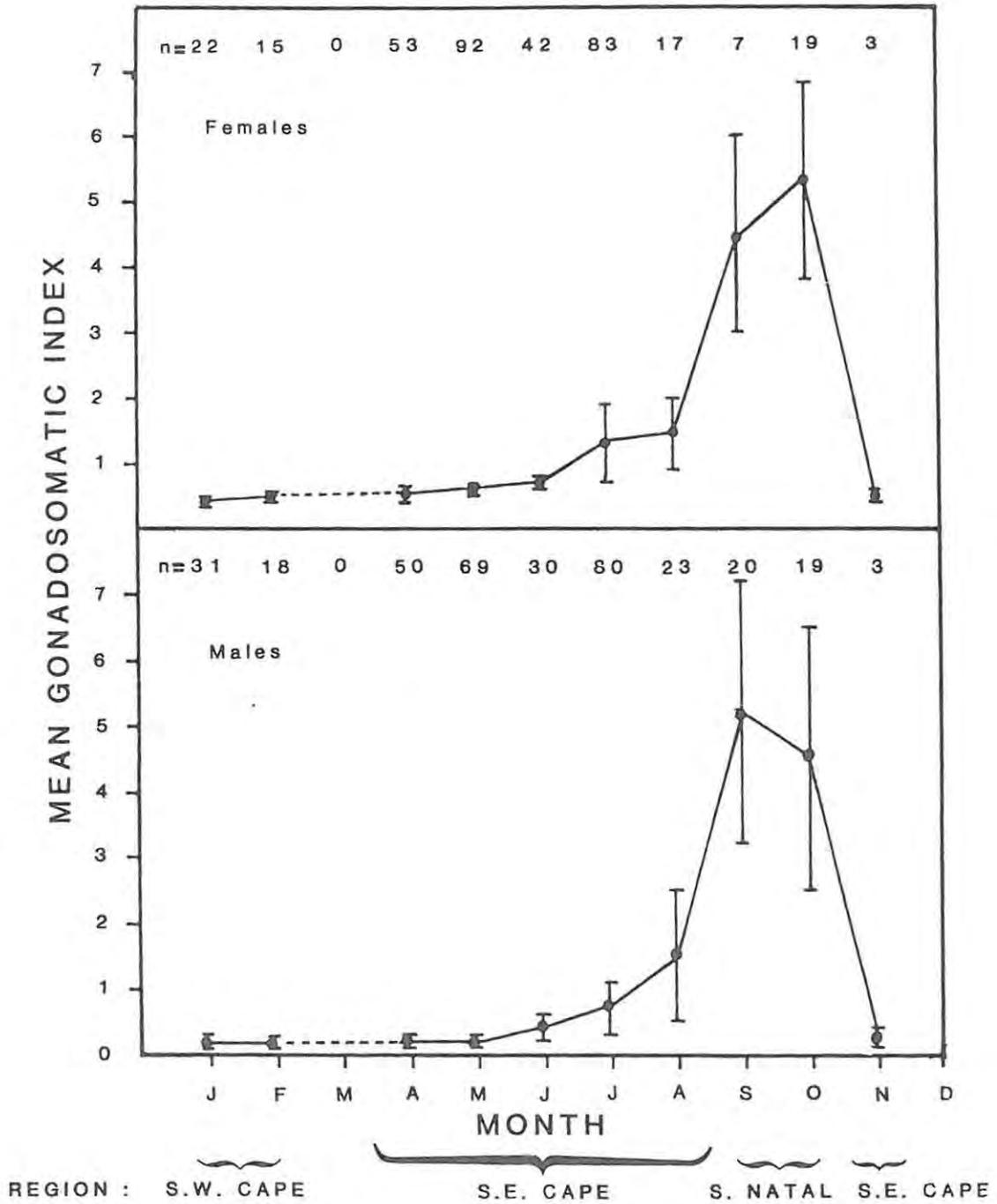


Figure 28. Mean monthly Gonadosomatic Indices calculated for male and female *Atractoscion aequidens* (>900 mm FL) along the South African eastern seaboard during 1985 to 1987.

1981).

Adult geelbek are dependent on pilchards, Sardinops ocellatus , as their primary source of food (see Chapter 6). The most likely reason for the reproductively premature occurrence of large geelbek in Natal could be attributed to the close association these fish have with their primary food source, which arrives along this part of the coast in June (Baird 1971, Crawford 1981b, Armstrong et al. 1987). As a result it may be concluded that the migration of A. aequidens to Natal is both gametic and alimental.

Since all data on fish in the breeding condition (Stage VI) were collected from southern Natal, it was difficult to accurately delineate the boundaries of the spawning ground. On account of the fact that geelbek are also caught in both northern Natal and southern Mozambique, it is reasonable to assume that spawning also occurs in these two regions. Spawning is unlikely to occur along the Transkei coast because, if conditions there were suitable, the fish would not necessarily move into Natal waters.

Figure 27 shows that spent fish (Stage VII) were almost completely absent from the Natal catches. Furthermore, ripe running fish (Stage VI) were not as well represented as would have been expected during the breeding season. The most probable explanation for these observations was that the fish move offshore to spawn, and then use the southward flowing Agulhas Current to aid their return to the Cape region.

Another explanation which could be advocated to explain the paucity of ripe running fish is based on the observation that feeding activity declines when breeding condition is attained. This phenomenon has been reported for numerous other species (Newsome & Leduc 1975, Foltz & Norden 1977, Pierce et al. 1980, Persons & Bulkley 1982, Savvatimskiy 1985). Circumstantial evidence for reduced feeding activity during the ripe and running stage comes from commercial fishermen in Natal who have reported the existence of large non-feeding shoals of geelbek during the

spawning season. This explanation alone, however, is insufficient as it does not explain the paucity of stage VII fish.

Figure 29 illustrates the mean monthly SFI's for geelbek sampled in the S.E. Cape and in Natal. This figure shows that there was a definite annual cycle in visceral fat accumulation. Comparison of Figures 27 and 28 revealed that the mean monthly SFI reached a peak just prior to significant increases in the weights of both male and female gonads. Furthermore, the predominantly ripe and ripe running fish examined in Natal contained virtually no fat. The latter observation was also confirmed by Garrat and Denton (ORI Durban, pers. comm.).

A depletion of accumulated lipid reserves, stored in various parts of the body, have been observed during the period of gonad maturation in many species of fish. These include: the herring, Clupea harengus (Wood 1958), the cod, Gadus morhua (Jangaard et al. 1967), the Cape hake, Merluccius capensis (Botha 1971), the Black Sea horsemackerel, Trachurus mediterraneus ponticus (Shchepkin 1971a), the scorpionfish, Scorpaena porcus (Shchepkin 1971b), the brook trout, Salvelinus fontinalis (Larson 1974), the perch, Perca fluviatilis (Craig 1977), the smelt, Osmerus mordax (Foltz & Norden 1977), the goldfish, Carassius auratus (Delahunty & de Vlammig 1980), the northern anchovy, Engraulis mordax (Hunter & Leong 1981), nine species of acanthurids (Fishelson et al. 1985), the alewife Alosa pseudoharengus (Flath & Diana 1985), and the roughhead grenadier, Macrourus berqlax (Savvatimskiy 1985).

Newsome & Leduc (1975) and Fishelson et al. (1985) have shown that the fat which is associated with the gonads of mature perch (Perca flavescens) and nine acanthurid species, was available only for gonadal maturation. In the surgeonfishes, the exclusive utilization of the fat reserves for gonadal maturation was found to be due to an intimate vascular system connecting the gonad and its fat bodies. In the geelbek the visceral fat is also both

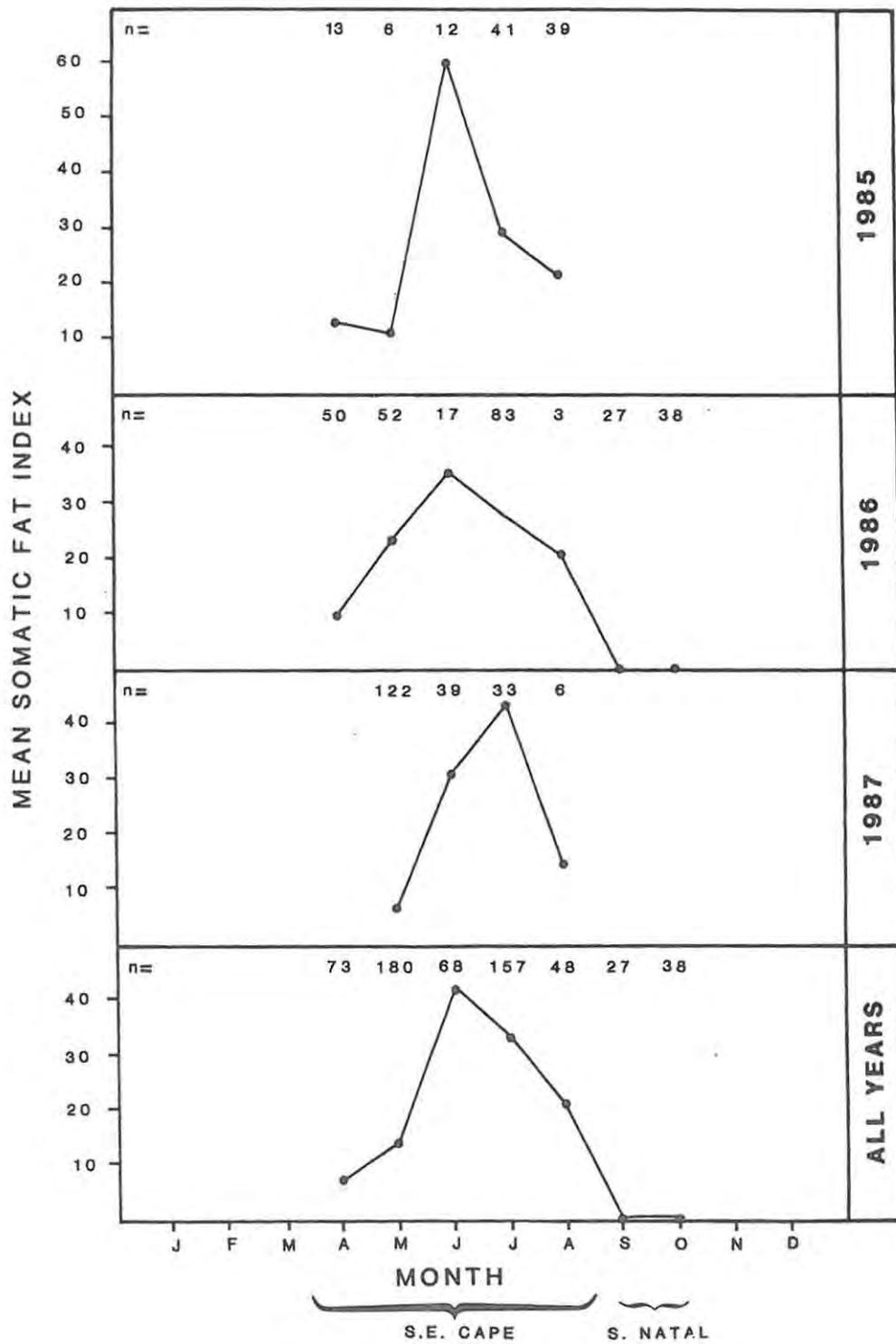


Figure 29. Mean monthly Somatic Fat Indices calculated for *Atractoscion aequidens* (>900 mm FL) along the South African eastern seaboard.

exclusively and intimately associated with the gonads (see Figs. 17 & 20). It could therefore be postulated that its purpose was likewise specifically for gonad development. Although energy reserves are also necessary for migration and maintenance (Greene 1913, Dotson 1978, in Guillemot *et al.* 1985, Glebe & Leggett 1981, McKeown 1984), the large lipid reserves in the liver and body musculature of the geelbek (Rapson *et al.* 1945) would most likely be used for this function.

Gonadosomatic indices may also be used as a rough estimate of reproductive investment or effort (Nikolskii 1963, Royce 1972, Moyle & Cech 1982). Figure 27 indicates that similar investments were made by both male and female fish. This observation will be discussed at the end of this chapter, in relation to the geelbek's general reproductive strategy.

Length and Age at Sexual Maturity

The percentage length frequencies of mature male and female geelbek sampled in the S.E. Cape are shown in Figure 30. Those from Natal are shown in Figure 31.

Both these figures indicate that the males and females attained sexual maturity at the same size. They also both illustrate that 100% maturity occurred between 960 and 990 mm FL. However, two different lengths at 50% maturity were obtained. Figure 30 indicates that 50% maturity was attained between 870 and 900 mm FL while Figure 31 suggests a length of between 900 and 930 mm FL. The latter value was taken to be more realistic as it was derived from fish sampled in the spawning area.

From the higher representation of lower size classes in Figure 30 it could be inferred that some of the younger fish do not migrate all the way to Natal. This conclusion is consistent with observations made in Chapter 3 that fish in the 840-900 mm size range were marginally better represented by northward migrating adult fish in the S.E. Cape, than by those which actually reach

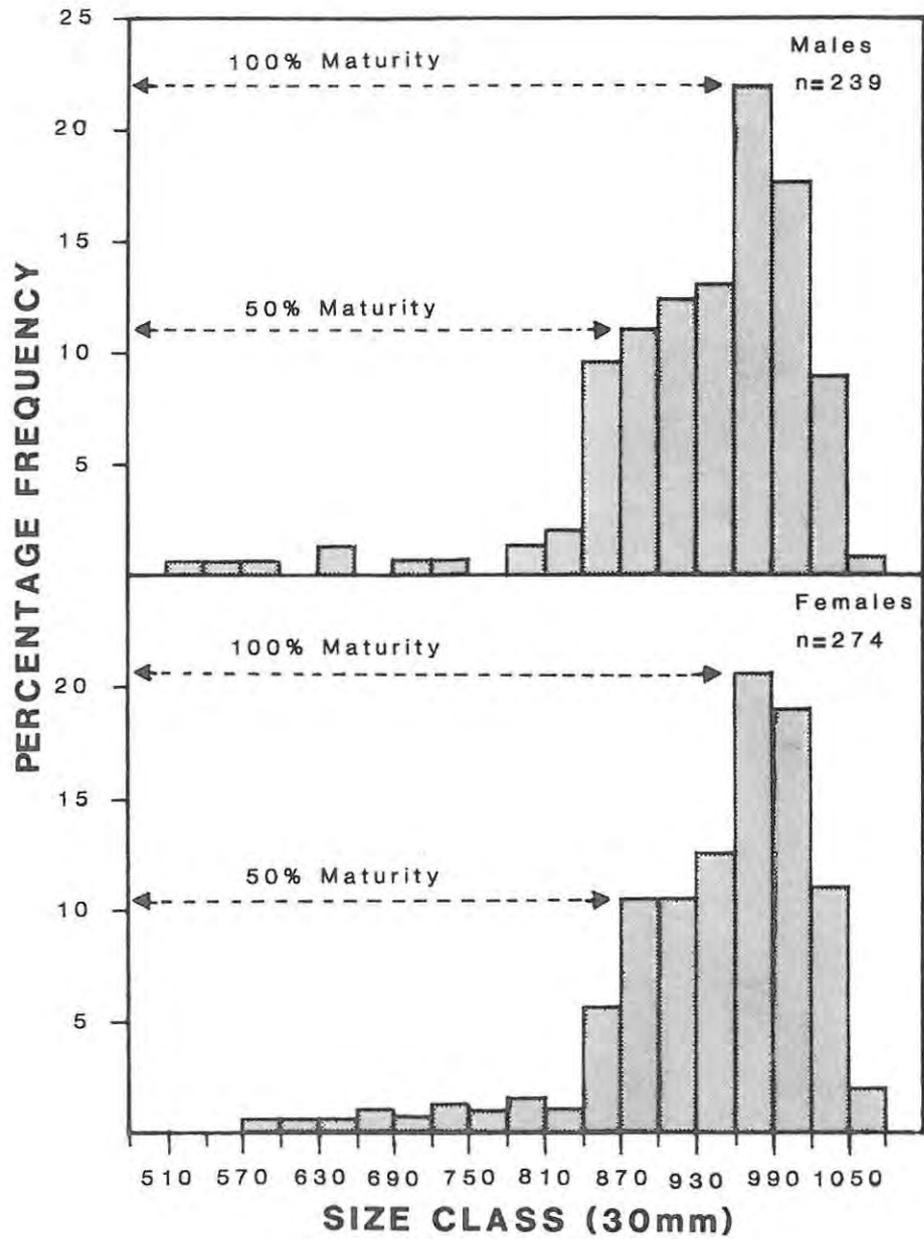


Figure 30. The percentage length frequency distribution of mature male and female *Atractoscion aequidens* measured in the South East Cape (1985-1987).

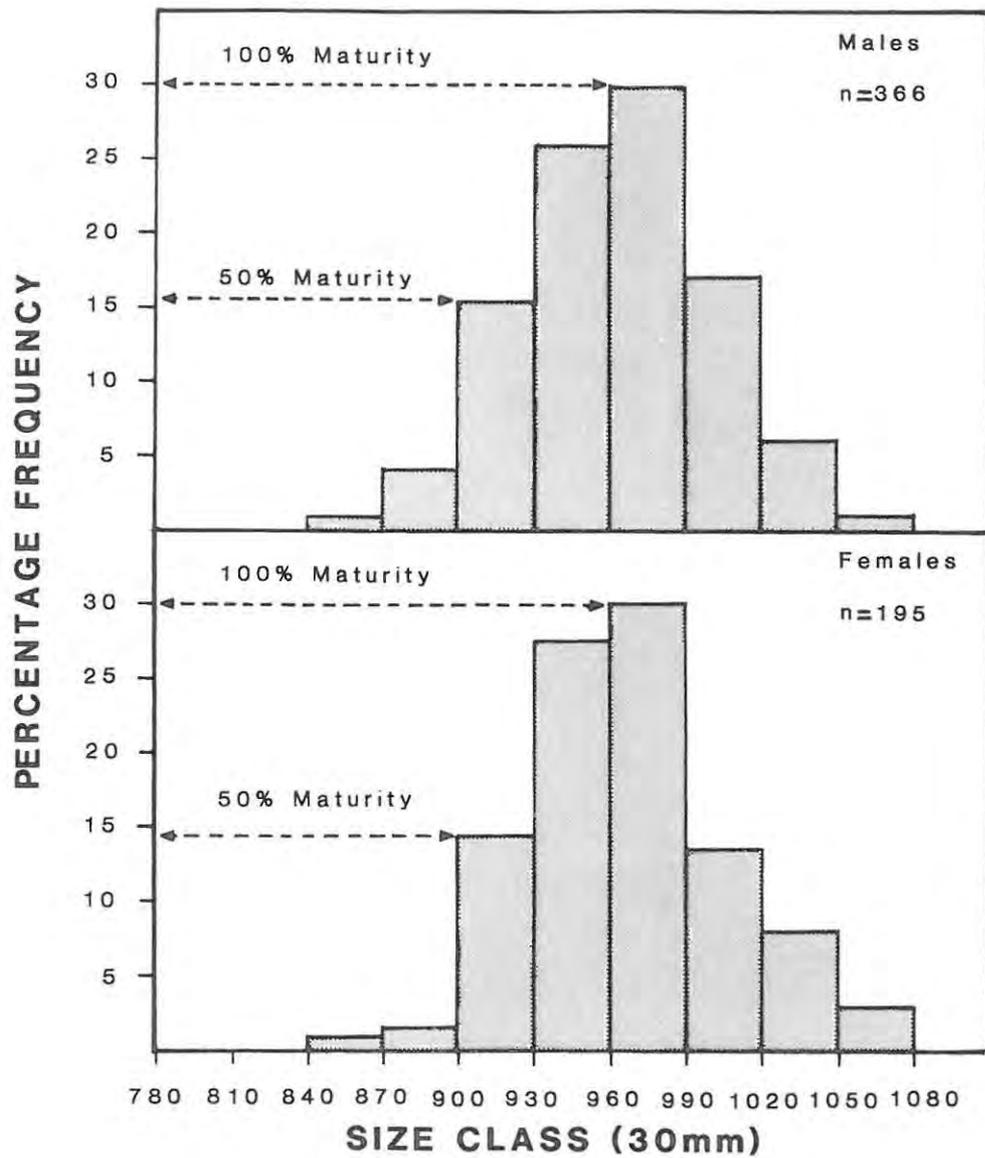


Figure 31. The percentage length frequency distribution of male and female *Atractoscion aequidens* sampled in Natal (1984-1986).

Natal. It was therefore assumed that gonad maturation was incomplete in those "adolescent" fish which do not reach the spawning ground. These two phenomena are not unique to A. aequidens. Harden-Jones (1968) presents evidence which suggests that some larger immature cod Gadus morhua also only undertake a partial migration to the adult spawning grounds. Incomplete gonad development has also been observed in Pomatomus saltatrix off the Natal coast (Van der Elst 1976).

In terms of age, 50% sexual maturity in A. aequidens is attained at an age of 5 years and 100% maturity at an age of 6 years (i.e. during their 6th and 7th year respectively).

Although the kob, A. hololepidotus, grows to a much larger size than A. aequidens (Van der Elst 1981, Heemstra 1986) it becomes sexually mature at a length of less than 250 mm TL (Smale 1985), and a corresponding age of one year or less (Wallace & Schleyer 1979, T. Hecht, Department of Ichthyology & Fisheries Science, Rhodes University, pers. comm.). It is also relevant to note that maturity in A. aequidens is attained at a length which is 82 per cent that of its asymptotic length. Using Smale's (1985) length-at-maturity and Wallace & Schleyer's (1979) L_{∞} , a value of 14 percent was calculated for A. hololepidotus. It could therefore be concluded that A. aequidens has a relatively large size and age at sexual maturity.

Sex Ratios

Table 6 gives the sex ratios and chi-square values for the various regions and size classes.

Chi-square analysis ($\chi^2_{0,05} = 3,84$) revealed that none of the sex ratios deviated significantly from unity. This result is consistent with the general theory regarding the sex ratios of animal populations (see Smith 1978).

Table 6. Sex ratios (male:female) of A. aequidens along the South African eastern seaboard

Region	Length Class (mm)	Ratio	n	χ^2
S.W. Cape	250-499	1:1.13	32	0,13
	500-749	1:1,07	354	0,4
	750-999	1:1	98	0
	1000 +	-	1	-
	TOTAL	1:1,06	485	0,26
S.E. Cape	250-499	1,04:1	1065	0,58
	500-749	1:1,09	274	0,52
	750-999	1,003:1	649	0,0015
	1000 +	1:1,4	63	1,9
	TOTAL	1,002:1	2051	0,006
Natal	TOTAL	1,36:1	62	2,3
All Regions	TOTAL	1:1	2598	0

Smale (1985), however, found a significant difference in the male:female ratio of 1:1,2. His results are attributed to a much lower sample number (n=612) and the fact that geelbek often form shoals which consist predominantly of one sex or the other (personal observation)

5.4 General Discussion and Conclusion

From the results presented in this chapter it was concluded that the migration of A. aequidens to Natal (see Chapter 3) is primarily for reproductive purposes and that spawning occurs in

this region in spring. As in many oceanodromous species (McKeown 1984) gonad recrudescence occurs en route. There is also evidence to suggest that some of the sub-adult or adolescent fish undergo a partial migration and incomplete gonad development.

The appearance of early juveniles (<390 mm FL) in the S.E. Cape in January, some two months after the breeding season and approximately 630 km down-current from the spawning area would indicate that eggs, larvae and juveniles are passively transported along the edge of the Agulhas Current. The core of the current travels at more than one meter per second (Pearce & Grundlingh 1982) and would cover the required distance in about 12 days. However, the slower peripheral waters, with associated counter currents, vortices and eddies (see Chapter 2), travel at more appropriate speeds (Grundlingh 1983, E. Schumann, Department of Oceanography, University of Port Elizabeth, pers. comm.). Apart from providing a means of transport, the waters of the Agulhas Current offer other advantageous features which may increase egg and larval survival. By being a few degrees warmer than the contiguous coastal waters (Pearce 1977, Christensen 1980) the current should enhance egg and larval development and thus reduce predation and mortality on these two vulnerable stages of the life cycle (Hunter 1981, Pitcher & Hart 1982). The water of the Agulhas Current also has an abundance of zooplankton (Berry 1978, Carter & Schleyer 1978) which the larval and juvenile geelbek could utilize as food. This planktonic food source may include the eggs and larvae of A. aequidens and possibly those of other species which also use the current at the same time and for the same purpose e.g. P. saltatrix (Van der Elst et al. 1976) and Lichia amia (Van der Elst 1981).

According to Holt et al. (1985) mass spawning at dusk is a common feature of sciaenid reproduction. Because eggs are allowed to disperse during the hours of darkness when they are less visible to planktivores which are also less active at this time, Holt et al. (op. cit.) suggested that this might be an adaptation to reduce egg predation. Mass spawning also has the advantage for

pelagic spawners in that it would maximize fertilisation and gamete recombination (Johannes 1978).

As a result of the preceding discussion it was postulated that geelbek spawn offshore during the evening in the peripheral waters of the Agulhas Current. Clearly, however, this hypothesis needs to be tested. The presence of drumming muscles in the males (Fig. 32) indicates that as in other sciaenids, male sound production might play a role in reproduction. These may either be used as in Gadus morhua for paired mating behaviour (Keenleyside 1979) or to assemble spawning shoals with sex ratios which are suitable for mass spawning.

It is hypothesized that after spawning the spent fish do not return inshore, but use the current to aid their return to the Cape. This would explain the paucity of stage VII fish in the Natal catches and also the absence of a "return run" off the S.E. Cape.

The inshore nature of the northward migration of both S. ocellatus (Baird 1971) and the geelbek, is believed to be due to the higher temperatures of the Agulhas Current, and more importantly, the resistance its southward flow would pose to their migration. It might also be possible that, by remaining inshore, they are able to use the current for orientation purposes (Harden-Jones 1968, McKeown 1984).

The conclusions reached in this chapter clearly show that the results presented by Smale (1985) on the reproductive biology of A. aequidens were largely inaccurate. This illustrates the dangers of speculating on inadequate information and emphasizes the need to study migratory species throughout their distributional range.

To obtain a general perspective on the reproductive strategy evolved by A. aequidens, the various components were examined in relation to Balon's (1975, 1984) classification of fishes based

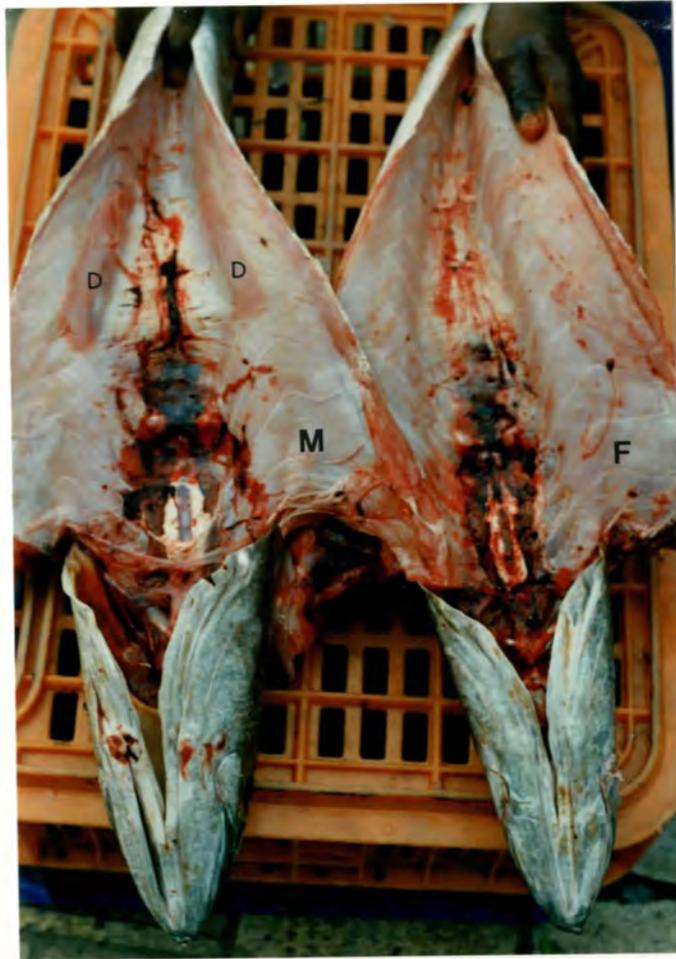


Figure 32. Example of a mature male (M) and a mature female (F) geelbek showing the presence of drumming muscles (D) in the lateral abdominal walls of the males and the absence of these muscles in the females.

on their reproductive styles. According to this classification, the geelbek is a typical example of the reproductive "guild" known as the "Pelagophils". The overall unifying feature of this group is that they are all pelagic, open water spawners. Further characteristics of this guild, which were also displayed by the geelbek, include: equal reproductive effort by both males and females, the development of large gonads (see Figs. 22 & 23) and a lack of external sexual dimorphism.

Although fecundity studies were not undertaken for the geelbek the pelagophils are generally a highly fecund species (Balon 1975). This is regarded as an adaptation to compensate for high egg and larval mortalities associated with their mode of reproduction (Balon op. cit., Hislop 1984). Because the growth rate of immature fish is higher than that of mature fish (Nikolskii 1963) and because fecundity is dependent on fish size (Nikolskii 1969), a late age at sexual maturity is expected to result in higher absolute fecundities at age, once maturity is attained. This would also result in higher absolute fecundities for the spawning individuals. The relatively late age at sexual maturity of the geelbek, may therefore be an important part of its reproductive strategy.

CHAPTER 6

FOOD AND FEEDING

6.1 Introduction

Fishes, like all organisms, are required to ingest food to obtain the energy and raw materials necessary for growth, reproduction, feeding and maintenance (Nikolskii 1963, Eckert & Randall 1983, Calow 1985).

"Optimal diet theory" predicts that a predator will select those prey which in terms of morphological, behavioural and physiological adaptations will maximise fitness in the evolutionary sense (Pyke *et al.* 1977, Krebs 1978, Hughes 1980, Townsend & Winfield, 1985). According to these authors, the selected prey are generally those which are energetically more profitable and thus provide the highest ratio of incoming energy to that expended by searching for and handling the prey.

Studies of diets based on stomach content analyses have contributed greatly towards the understanding of the autecology, growth and ecological roles of fish populations (Windell & Bowen 1978, Pitcher & Hart 1982). Autecological aspects which are revealed by stomach contents include predator-prey inter-relationships, vertical and horizontal movements, competition between species and the degree of adaptability to changes in food abundance and type (Pinkas *et al.* 1971, Hickey 1975).

Economically desirable carnivores have been the subjects of the majority of feeding studies (Pinkas *et al.* 1971). However, due to difficulties in identifying well digested prey, feeding studies on South African top marine predators have until recently been neglected (Smale 1986).

Three studies have previously been undertaken on the feeding biology of the geelbek. Nepgen (1982) examined 82 stomachs

containing food, collected from fish caught in False Bay between mid-spring of 1979 and mid-autumn of 1980. Stomach contents were analysed using the frequency of occurrence method only. A shortcoming of this study was that Nepgen (op. cit.) only used one of several methods of stomach content analysis (see later). Buxton et al. (1984) examined the stomach contents of 18 geelbek ranging between 72 and 393 mm FL, which were trawled mainly in Algoa Bay. Finally, Smale (1986) analysed the food of 59 fish which varied from 345 mm to 970 mm FL. These were caught chiefly in the Port Elizabeth area between February 1978 and May 1982.

The objectives of the present investigation were to establish the temporal, spatial and size related diets of A. aequidens and also to determine what these revealed about the migratory behaviour and evolution of this species.

6.2 Materials and Methods

Out of a total of 1861 stomachs examined from the Port Alfred area 272 were found to contain prey items. Food was found in 46 of the 586 stomachs inspected in the Gordons Bay area. Other than bait, no gut contents were found in any of the 63 fish examined in Natal.

Stomach contents were processed fresh and as soon as possible after capture, as both preservatives and gastric juices were found to quickly erode the more delicate prey items. The contents of each stomach were identified to the lowest possible taxon, counted and weighed (wet) to the nearest 0,1 g. Bait was easily recognized and discarded. Fish, which constituted the majority of the contents, were either identified whole, or by comparing sagittal otoliths with reference material in the Department of Ichthyology and Fisheries Science at Rhodes University. The greatest number of either left or right otoliths in each stomach were used to calculate the number of ingested fish. Cephalopods were identified by means of their beaks by the Prey Identification Service of the Port Elizabeth Museum.

The four most commonly used methods of stomach content analysis are those based on frequency of occurrence, percentage composition by number, percentage composition by volume and percentage composition by weight (Pinkas *et al.* 1971, Hecht 1976, Windell & Bowen 1978, Buxton 1984, Marais 1984, Garrat 1984, Smale 1986). These may also be combined to calculate indices of relative prey importance (Hyslop 1980).

Hyslop (*op. cit.*) reviewed the literature on stomach content analyses and concluded that no single method would give a complete picture of dietary importance. He also stated that at least one method measuring the amount and one measuring the bulk of food should be used. The quantitative data pertaining to each geelbek prey type were processed using three methods. These were percentage frequency of occurrence (%F) (Hynes 1950), numerical percentage contribution (%N) (Pillay 1952) and percentage by mass (%M) (Windell 1968). The results from all three methods were combined and an index of relative prey importance (IRI) was calculated:

$$\text{IRI} = (\%N + \%M) \times \%F$$

This is a modification of the IRI used by Pinkas *et al.* (1971) where prey volume was used instead of mass.

While collecting stomachs for analysis in Port Alfred, it was noticed that the number of fish with stomachs containing food appeared to decline after the first arrival of adult fish in April. To confirm these observations monthly percentages of stomachs containing food as well as major prey organisms (see later) were calculated for this area.

6.3 Results and Discussion

Figure 33 shows the length frequency distribution of geelbek with stomach contents in the S.E. and the S.W. Cape. Considering the

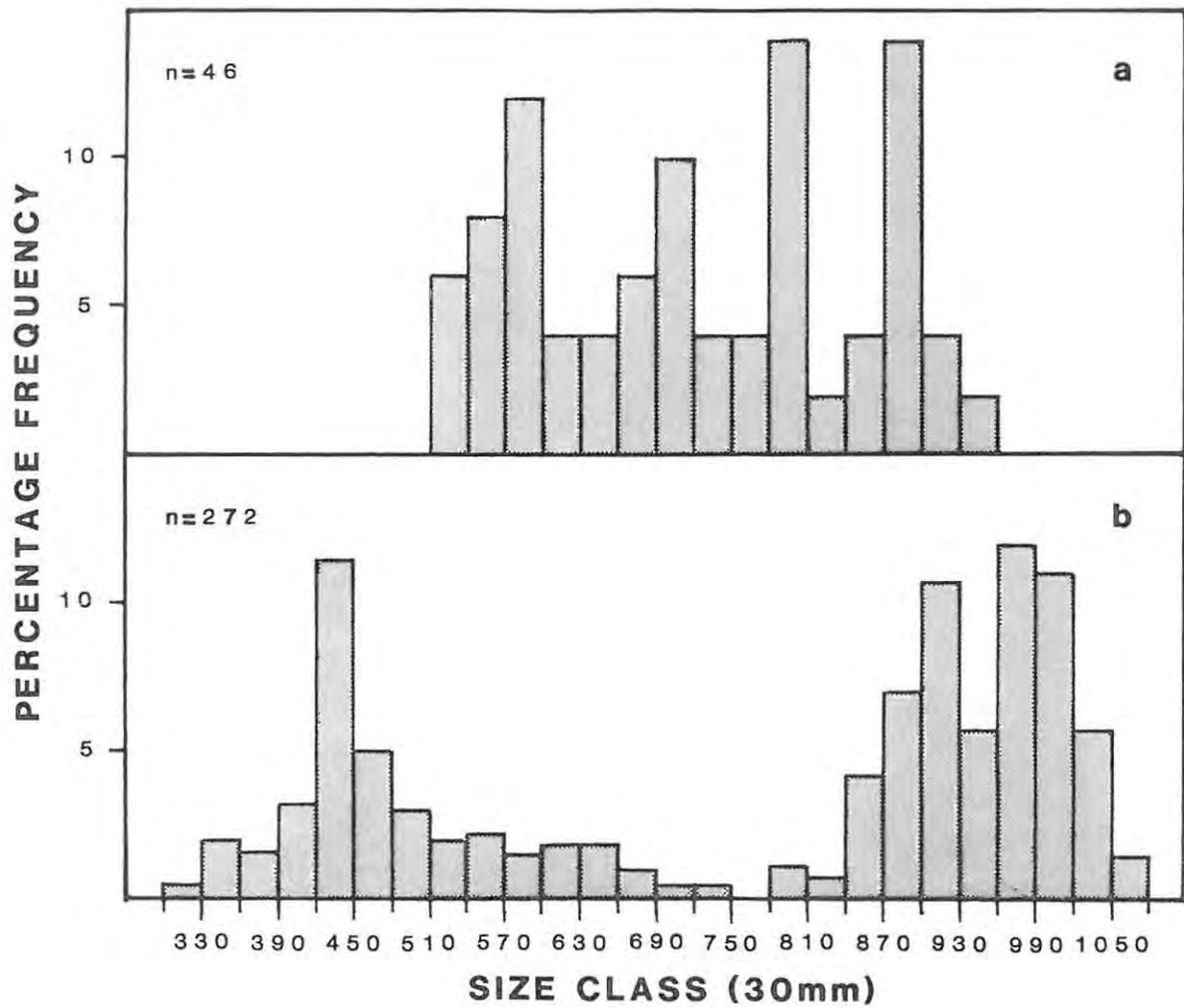


Figure 33. Fork length frequency distribution of Atractoscion aequidens examined with stomach contents from a) the South West Cape and b) the South East Cape.

overall length distribution of the fish containing food in their stomachs in the S.E. and S.W. Cape, it can be assumed with a reasonable measure of confidence that the results of the stomach content analyses reflect the prey of the geelbek population as a whole.

Tables 7 and 8 present the results of the stomach content analyses from the S.E. Cape and S.W. Cape respectively. Figure 34 shows the percentage composition of the principal dietary items in the S.W. and S.E. Cape regions. Results of the size related analyses in the S.E. and S.W. Cape are given in Tables 9 and 10 respectively. Figure 35 shows the monthly percentages of stomachs containing food in the S.E. Cape area. Percentages of stomachs of fish, above and below 750 mm FL, containing the principal prey items, viz. Sardinops ocellatus, Engraulis capensis (Clupeidae) and Trachurus trachurus (Carangidae), are depicted in Figure 36.

Tables 7 and 8 revealed that although a relatively wide range of prey species were taken by geelbek their diets in both regions consisted predominantly of S. ocellatus, E. capensis and T. trachurus. Based on the index of relative prey importance and the results of all three methods of analysis, the single most important food item in the S.E. Cape was S. ocellatus and in the S.W. Cape, E. capensis (Tables 7 & 8 and Fig. 34). Despite the lack of stomach contents from fish in Natal, numerous geelbek personally caught off the shore and speared along the Natal south coast during the late winter of 1979 and 1982 were found to contain S. ocellatus.

As pointed out by Payne et al. (1987) composite indices are particularly useful in comparing dietary changes with growth. Indices of relative prey importance in Table 9 indicated that in the S.E. Cape, E. capensis is considerably more important in the diets of smaller geelbek (<750 mm FL) than in those which are greater than this length. This table also shows that the relative importance of T. trachurus increased with predator size

TABLE 7. Stomach content analysis of Atractoscion aequidens from the S.E. Cape. The totals refer to number of items (N), prey wet mass (M) and number of stomachs (F).

Prey	1985				1986				1987				All Years			
	%N	%M	%F	IRI	%N	%M	%F	IRI	%N	%M	%F	IRI	%N	%M	%F	IRI
PISCES																
<u>Sardinops ocellatus</u>	34,0	37,0	27,6	1460,0	75,0	71,0	76,0	11096,0	57,0	42,0	52	5148,0	62,0	56,0	53,0	6254,0
<u>Engraulis capensis</u>	32,0	15,0	27,0	1269,0	6,0	2,0	12,0	96,0	22,0	3,3	31	936,18	16,0	3,3	26,0	501,8
<u>Trachurus trachurus</u>	7,0	25,0	12,0	384,0	3,0	20,0	9,0	207,0	6,7	45,0	15	775,0	5,0	31,0	12,0	432,0
<u>Etrumeus teres</u>	7,8	13,0	12,3	256,0	4,0	1,1	6,1	31,0	5,0	3,0	11	88,0	4,7	3,0	10,0	77,0
<u>Merluccius capensis</u>					1,0	0,2	3,0	3,6					0,4	0,1	1,1	0,5
<u>Pomatomus saltatrix</u>					0,3	0,6	1,0	0,9					0,1	0,3	0,4	0,2
<u>Argyrozona argyrozona</u>	1,0	1,0	1,5	3,0									0,1	<0,1	0,4	
<u>Pterogymnus lanarius</u>									0,4	3,7	1,0	4,0	0,1	1,6	0,4	0,6
Serranidae	1,0	0,3	1,5	2,0									0,1	<0,1	0,4	
Triglidae					0,3	0,2	1,0	0,5					0,1	0,1	0,4	<0,1
Ophidiidae	1,0	0,17	1,5	1,8									0,1	0,6	0,4	0,2
<u>Diplodus cervinus capensis</u>									0,4	1,3	1,0	1,7	0,1	<0,1	0,4	
Unidentified Fish	8,0	0,7	13,0	113,0	8,9	1,6	9,0	94,0	10,3	0,8	8,0	88,8	9,5	1,2	10,0	107,0
MOLLUSCA																
<u>Loligo reynaudi</u>	2,0	6,8	3,0	26,0	1,0	3,0	2,0	8,0					0,7	2,0	1,5	4,0
Sepiidae					0,3	0,2	1,0	0,5					0,1	0,1	0,4	<0,1
CRUSTACEA																
<u>Squilla armata</u>	1,0	<0,1	1,5										0,1	<0,1	0,4	
Mysidacea	3,8	<0,1	3,0										0,6	<0,1	0,7	
TOTALS	103	1247	65		347	9460	98		272	8159	109		722	18866	272	

TABLE 8. Stomach content analysis of Atractoscion aequidens from the S.W. Cape. The totals refer to number of items (N), prey wet mass (M) and number of stomachs (F).

Prey	1986				1987				All Years			
	%N	%M	%F	IRI	%N	%M	%F	IRI	%N	%M	%F	IRI
PISCES												
<u>Engraulis capensis</u>	62,0	22,0	58,0	4872	84,0	17,2	54,0	5465	72,0	20,0	57,0	5244,0
<u>Sardinops ocellatus</u>	23,0	43,0	37,0	2442					10,4	20,0	15,2	462,0
<u>Trachurus trachurus</u>	8,0	17,0	29,0	725	4,0	8,2	13,6	166	6,0	13,0	22,0	418,0
<u>Sarpa salpa</u>	1,1	17,0	4,0	75	5,4	54,6	4,5	270	3,0	35,0	4,3	163,0
<u>Pomatomus saltatrix</u>					18,0	20,0	5,4	205	2,4	10,0	9,0	111,6
<u>Hepsetia breviceps</u>					1,3	<0,1	4,5	6	1,3	-	2,2	2,9
<u>Etrumeus teres</u>	4,4	4,7	8,3	75					2,4	2,5	4,3	21,0
CRUSTACEA												
<u>Squilla armata</u>	5,5	<0,1	12,5	68					3,0	<0,1	6,5	19,0
TOTALS	90	100	24		74	907	22		164	1908	46	

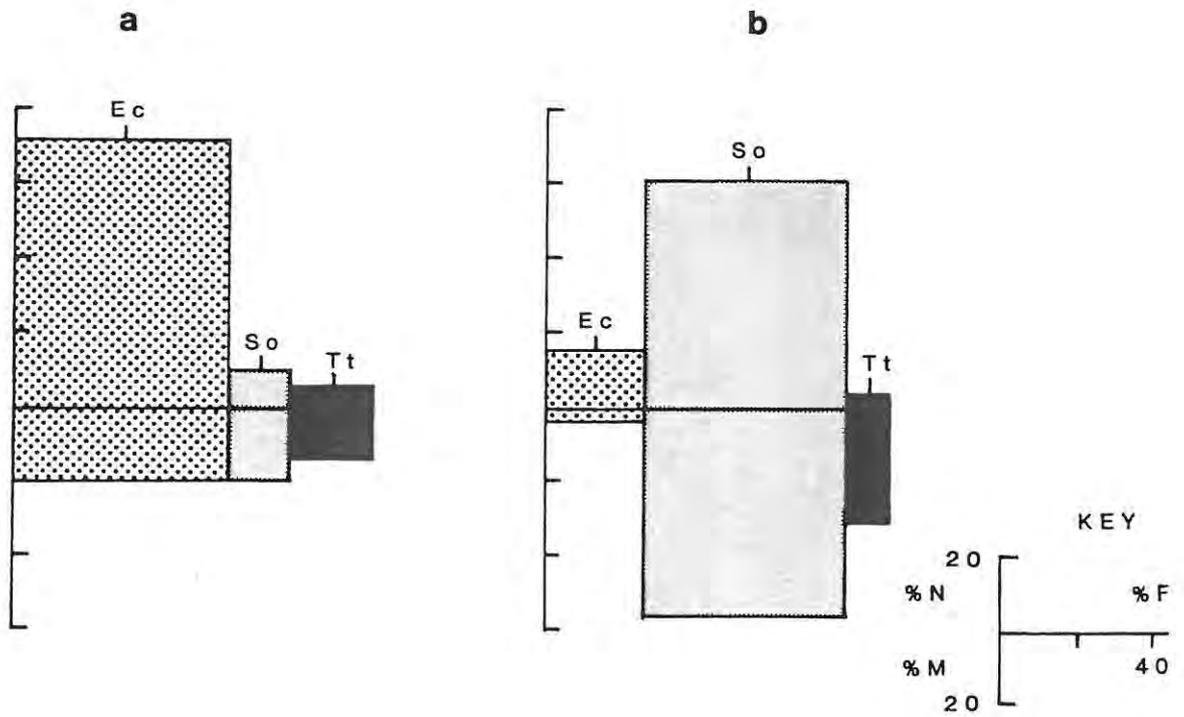


Figure 34. The composition of the principal prey species of *Atractoscion aequidens* in a) the South West Cape and b) the South East Cape. Ec : *Engraulis capensis*, So : *Sardinops ocellatus*, Tt : *Trachurus trachurus*.

TABLE 9. Stomach content analysis of A. aequidens from the S.E. Cape according to predator size. The totals refer to number of items (N), prey wet mass (M) and number of stomachs (F).

Prey	Predator Fork Length											
	250-499mm				500-749mm				750mm +			
	%N	%M	%F	IRI	%N	%M	%F	IRI	%N	%M	%F	IRI
PISCES												
<u>Sardinops ocellatus</u>	28,5	60,0	30,0	2670,0	40,0	50,0	30	2700	70,0	57,0	66,0	8382,0
<u>Engraulis capensis</u>	44,0	21,0	39,0	2535,0	48,0	17,0	70	4480	7,2	1,7	13,3	118,0
<u>Trachurus trachurus</u>	1,0	2,0	1,4	4,2	1,6	14,0	4	62	6,0	34,0	18,0	720,0
<u>Etrumeus teres</u>	13,3	19,0	8,0	258,0	3,2	2,0	4	21	3,4	2,0	7,5	40,0
<u>Merluccius capensis</u>									0,5	0,1	1,7	1,0
<u>Pomatomus saltatrix</u>									0,2	0,3	0,6	0,3
<u>Argyrozoona argyrozoona</u>									0,2	<0,1	0,6	0,1
<u>Pteryogymnus lanianus</u>									0,2	1,8	0,6	1,2
Serranidae									0,2	<0,1	0,6	0,1
Triglidae									0,2	0,1	0,6	0,2
Ophidiidae									0,2	<0,1	0,6	0,1
<u>Diplodus cervinus</u>												
<u>capensis</u>					1,6	11,4	4	52				
Unidentified Fish	7,1	3,6	10,0	107,0	3,2	0,2	8	27	10,5	1,2	10,4	121,0
MOLLUSCA												
<u>Loligo reynaudi</u>					3,2	17,0	4	80	0,5	1,2	1,7	3,0
Sepiidae	1,0	2,2	1,4	5,0								
CRUSTACEA												
<u>Squilla armata</u>	1,0	<0,1	1,4	14,0								
Mysidacea	4,0	<0,1	2,8	11,2								
TOTALS												
	98	849	72		62	969	27		561	16838	173	

TABLE 10. Stomach content analysis of A. aequidens from the S.W. Cape according to predator size. The totals refer to number of items (N), prey wet mass (M) and number of stomachs (F).

Prey	Predator Fork Length							
	500 - 749 mm				750 mm +			
	%N	%M	%F	IRI	%N	%M	%F	IRI
PISCES								
<u>Engraulis capensis</u>	79,0	30,3	66,6	7280,0	63,0	17,0	50	4000,0
<u>Sardinops ocellatus</u>	8,0	22,5	12,5	381,0	13,0	19,0	20	640,0
<u>Trachurus trachurus</u>	4,0	27,0	16,6	514,6	8,0	8,7	30	501,0
<u>Sarpa salpa</u>	2,2	8,7	8,3	90,0	6,6	45,0	10	516,0
<u>Pomatomus saltatrix</u>				-	2,6	10,0	10	126,0
<u>Hepsetia breviceps</u>	1,0	0,2	4,0	5,0	1,3	-	5	6,5
<u>Etrumeus teres</u>	4,5	11,0	8,3	128,6				
CRUSTACEA								
<u>Squilla armata</u>	1,0	<0,1	4,0	4,1	5,2	<0,1	10	52,6
TOTALS	90	425	24		75	1484	22	

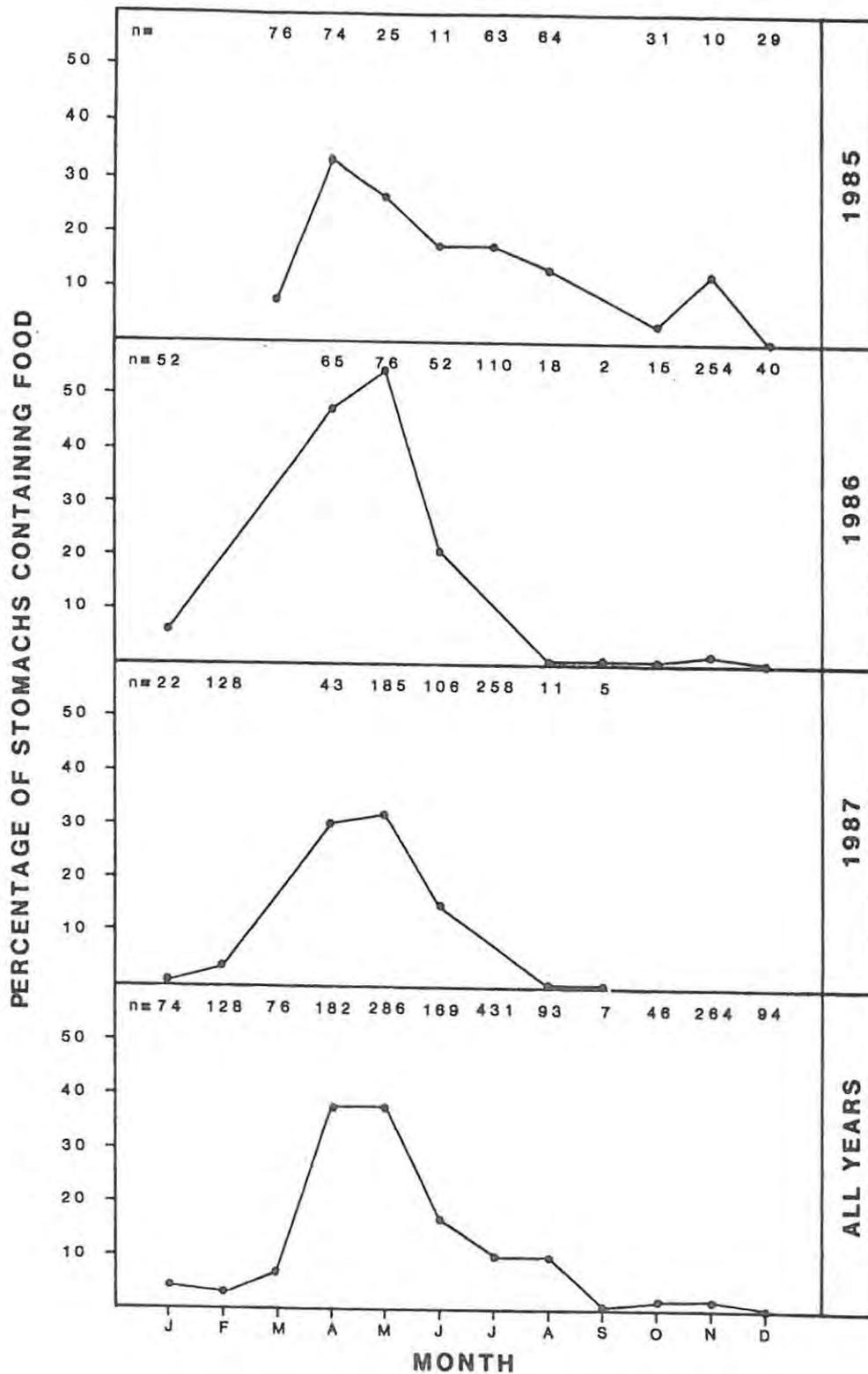


Figure 35. The monthly percentage of *Atractoscion aequidens* stomachs sampled in the South East Cape (Port Alfred), which contained food. The n values refer to the number of stomachs examined.

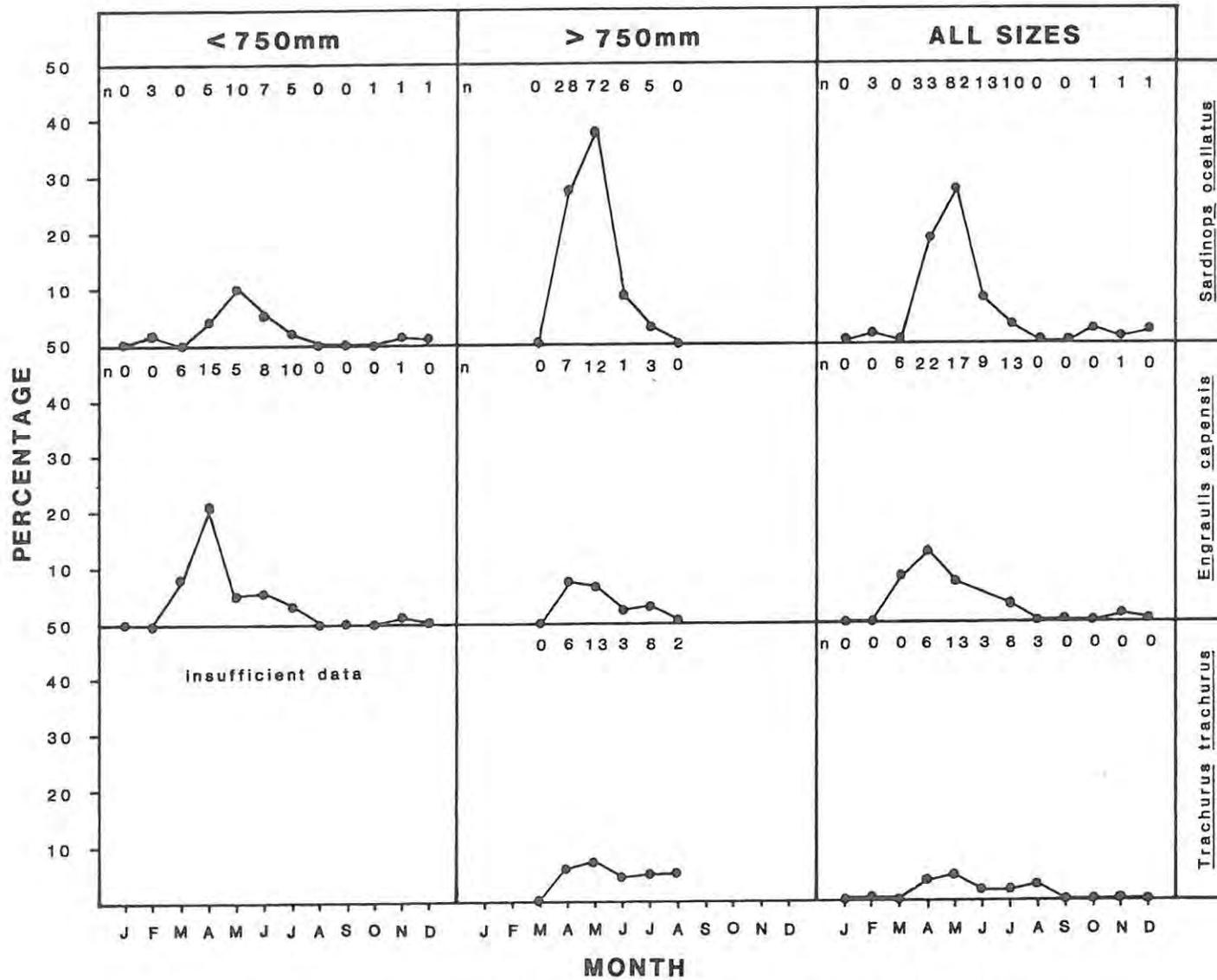


Figure 36. The percentage of *Atractoscion aequidens* stomachs, from fish above and below 750 mm FL, containing remains of the principal prey items. The n values refer to the number of stomachs containing prey items.

and that they were mainly consumed by geelbek greater than 750 mm FL. Although S. ocellatus was important in all three size classes, shown in Table 9, it was of greater importance in the largest size group.

These predator length related dietary variations are largely attributed to the size of the prey which generally increases in accordance with that of the predator (Marcotte & Browman 1986). A rough idea of specific prey sizes was obtained from direct measurements of partially digested food. The average total length of geelbek prey in the S.E. Cape were: E. capensis - 115 mm (n=22), S. ocellatus - 185 mm (n=31) and T. trachurus - 453 mm (n=6).

The average size of, T. trachurus 125 mm TL (n=3), consumed in the S.W. Cape was considerably smaller than those ingested in the S.E. Cape. It is therefore not surprising that similar IRI values were obtained for T. trachurus consumed by both predator size groups found in the S.W. Cape region (Table 10). Even though E. capensis proved to be the most important prey species for both S.W. Cape size groups shown in Table 10, it is considered noteworthy that as in the S.E. Cape, more anchovy were consumed by geelbek below 750 mm FL than by those greater than this length. Also consistent with the S.E. Cape trend, was the fact that more S. ocellatus were consumed by the largest (750+ mm FL) size group (see Tables 9 & 10).

The results of this study are generally consistent with those published by other authors on the feeding of A. aequidens within comparable size ranges. Using the frequency of occurrence method, Nepgen (1982) found E. capensis to be the most dominant species in the stomachs of geelbek from False Bay. He did, however find that the cephalopod Loligo reynaudi was also a substantial dietary component. No squid were found in the stomachs of A. aequidens in the S.W. Cape during the present study. The present study also substantiated the feeding trends observed for geelbek in the S.E. Cape by Smale (1986). Smale

(op. cit.) found that S. ocellatus was the most important prey species in this region. He also showed that T. trachurus was consumed by larger fish and that there was an increase in the proportion of E. capensis ingested by smaller individuals.

Buxton et al. (1984) found that mysids were the most important prey item for trawled A. aequidens between 72 mm and 393 mm FL. Due to the 378 mm FL (400 mm TL) size limit and gear selectivity only a few fish of this size range were sampled during the present study. This illustrates the limitation of using commercially and recreationally caught linefish for feeding studies (see also Smale 1983). Nevertheless, Table 9 does show that although taken in limited quantities, mysids were only consumed by the smallest size class (250-500 mm FL).

At the end of his review Hyslop (1980) concluded that the differential digestion of prey items is a potential source of bias in all currently used methods of stomach content analysis. However, one would expect that pilchards and anchovies, which together constitute most of the food ingested by the geelbek, to be digested at relatively similar rates. Particularly when considering that many predators have more diverse diets which often include prey species (such as crustaceans and molluscs) with slow digesting hard exoskeletons (Berg 1979, Smale & Bruton 1985).

The regurgitation of stomach contents (also encountered by many other workers) (Pinkas et al. 1971, Van der Elst 1976, Garrat 1984, Smale 1983, Bowman 1986), proved to be a hindrance during this study. However, the fish within each region were caught, throughout the year on the same fishing grounds and corresponding depths. Differential regurgitation as a result of barotrauma was therefore unlikely to have occurred in any one region and hence could not have biased the results. This is particularly relevant when considering qualitative and quantitative temporal fluctuations of food type.

Figure 35 revealed a seasonal trend in the quantities of food eaten by geelbek in the Port Alfred area. The percentages of stomachs containing food reached a peak in April/May of each year. Figure 36 shows that this trend was a result of temporal variations in the consumption of S. ocellatus and E. capensis.

As shown in Chapter 3, A. aequidens in the S.E. Cape have a bimodal size distribution. Those above 750 mm FL are represented by shoals of northward migrating fish with elevated energy demands while those below this length are generally south bound juveniles of less than one year. Figure 36 shows that the above mentioned feeding trend occurs in both these size groups, which implies that it was a function of prey availability in the S.E. Cape and not selection in compliance with energy requirements. A review of the relevant literature was undertaken in an attempt to establish whether the movements of prey played a role in the feeding frequency of the geelbek. Fortunately, because of their economic importance a substantial amount of work has been undertaken on the biology and movements of both pilchard and anchovy along the South African coast.

Anchovy are most abundant in the S.W. Cape during the summer months (Crawford 1981a) where they become concentrated inshore by the advection of warm Agulhas Bank surface water (Armstrong et al. 1985). During early autumn they move eastwards and out of this region (Crawford op. cit., Hampton 1987). This migration coincides with an eastward coastal movement of cool water (Christensen 1980, Shelton et al. 1985).

The catches of A. aequidens in the S.W. Cape are highest during summer and tail off in April (see Chapter 3), thus indicating a close correlation between the occurrence of this species and its major food source. The majority of the geelbek in this region are sexually immature and do not partake in the spawning migration (see Chapters 3 & 5). It is therefore probable that these fish follow the movements of their prey. No attempt has been made at defining the limits of the anchovy migration and

unfortunately no length measurements of geelbek were obtained from the more southerly areas of the S. Cape. However, unpublished SFRI linefish records have shown that catches of geelbek at Stilbaai and Mossel Bay are relatively low (Fig. 3). As mentioned previously, communication with fishermen and limited length measurements have indicated that the length frequencies of fish from the Plettenberg Bay/Knysna area are more similar to those of the S.E. Cape than those of the S.W. Cape. It is therefore suggested that as the cooler water moves further eastward and seaward, both predator and prey become more dispersed moving out over the eastern Agulhas Bank and away from the fishing grounds of the S. Cape line-fishermen. Relaxation of the advective process during autumn and winter increases the available area on the Agulhas Bank for plankton production which, is usually higher on the eastern side (Shelton et al. 1985, Armstrong et al. op. cit.). A progressive warming of the Bank in spring (Armstrong et al. 1987) would presumably result in the return of both geelbek and anchovy to the S.W. Cape where by summer they would once again be concentrated in the coastal zone within the range of the fishermen.

The snoek (Thyrsites atun) on the west coast of South Africa exhibits a similar migratory pattern which is also related to seasonal patterns of E. capensis availability (Crawford & De Villiers 1985).

Although pilchard recruits and the older fish are found on the South African west coast, the young adults display a similar migratory pattern in the S.W. Cape to adult anchovy (Crawford 1981b, Armstrong et al. 1985). They do, however differ in that the autumn eastward migration is far more extensive, ultimately reaching Natal in June/July to form the annual "sardine run" (Baird 1971, Crawford 1981b, Armstrong et al. 1987). By winter the previously mentioned insertion of cooler water expands to form a band which virtually extends along the entire South African eastern seaboard (Baird 1971, Christensen 1980), thus providing a possible conduit for this migration.

There is evidence to suggest the existence of pilchard and anchovy stocks in the S.E. Cape. Anders (1975) recorded spawning in both species along the Cape east coast. Smale (1983) observed that S. ocellatus and E. capensis are important prey of pelagic predators during the entire first half of the year. In addition the stomach contents of gannets (Morus capensis) from Bird Island (Algoa Bay) reflect a similar trend (W. Maritz, unpublished data, Port Elizabeth Museum). Hydrologically, the occurrence of regular upwelling in the S.E. Cape, coupled with corresponding temperature reductions and chlorophyll production (Schumann et al. 1982, Shannon et al. 1984) support the existence of these shoals.

The decline of S. ocellatus and E. capensis in the diets of predators in the S.E. Cape during winter, would indicate that these fish leave the region during this period. It is probable that they join the pilchards arriving with the cooler water from the S.W. Cape and join the latter in their migration to Natal. It is also possible that some E. capensis from the former region also take part in this migration, as these two species often shoal together (Armstrong, SFRI, pers. comm.).

Geelbek in the S.E. Cape seem to take advantage of the concentrated shoals of migrating prey species which would adequately explain the observed feeding trends. The geelbek is not the only species to opportunistically feed on this readily available food source. Hecht (1976) observed a dramatic increase in the amount of S. ocellatus ingested by the Cape hake (Merluccius capensis) off Port Elizabeth during May and June in two consecutive years.

Figure 36 indicates that horse-mackerel, T. trachurus were only consumed from April to August in the S.E. Cape. It is suggested that this was not a function of prey availability, but was rather due to the fact that geelbek large enough (>750 mm) to consume the S.E. Cape horse-mackerel are only present in this

area during the above-mentioned period (see Chapter 3). Furthermore, Hecht (1976) revealed that there is little seasonal variation in the abundance of T. trachurus off Port Elizabeth. It is also generally accepted that the eastern Cape horse-mackerel represent a separate stock from those in the western Cape (Crawford 1980, Hecht, (in prep.)).

A comparison of Figure 35 with Figure 29 in Chapter 5 revealed that peak feeding occurred just prior to the accumulation of gonadal fat reserves. Both Nikolskii (1963, 1969) and Shul'man (1974, in de Vlaming et al. 1978) concluded that fattening cycles in fishes are closely tied to seasonal variations in food availability. Since it is generally accepted that the seasonal cycle of events in the mode of life of fishes has adaptive significance (Nikolskii 1963), the observed feeding trend in A. aequidens is suggested to play an important role in its reproductive cycle. This is substantiated to a degree by correlations between reproductive success and the amount of fat accumulated in other species of fish (Dahlberg 1969, in Pierce et al. 1980, Newsome & Leduc 1975, Tyler & Dunn 1976, Craig 1977, Pierce et al. op. cit.).

Energy reserves also play a role in the lives of sexually immature geelbek. Rapson et al. (1945) found that liver lipids of geelbek from the False Bay area were highest in summer and early autumn and lowest in spring. These results correlate well with the previously discussed trends in the concentration and dispersal of E. capensis. It is of interest to note that the accumulated fat reached a minimum in spring in both mature and immature geelbek even though these two groups are engaged in completely different activities.

The advantages of energy stores are that they improve the efficiency of energy utilization in situations where there is significant seasonal variation in prey availability (Mackinnon 1972) or in the physiological energy demands e.g. during gonadal development. They would also be expected to buffer the effects

of short term fluctuations in food consumption on gonad development.

Pilchards, anchovies and horse-mackerel belong to a group of fishes known as obligate schoolers which maintain themselves in coherently polarized shoals even in the presence of danger (Breder 1967). There is a great deal of literature indicating that shoaling in species such as these has anti-predatory advantages (eg. Brock & Riffenburgh 1960, Breder 1967, Iversen 1967, Radakov 1973, Major 1977, Burgess & Shaw 1979, Partridge 1982). However, these advantages are reduced by those predators which also form schools and display co-ordinated hunting activity (Iversen 1967, Hobson 1968, Radakov 1973, Major 1977, Burgess & Shaw 1979, Potts 1981). The geelbek which is almost always encountered in shoals (personal observations and communication with fishermen) is expected to fall into this category. Furthermore, after observing co-ordinated hunting behaviour in yellowtail (Seriola lalandi), Schmitt & Strand (1982) concluded that all fish which primarily consume open water schooling species are likely to foster co-operative foraging behaviour.

Geelbek have been observed to form densely packed rotating ring shaped shoals in the vicinity of S. ocellatus (personal diving observation). It is postulated that A. aequidens encircle and ingest their prey, possibly at the water surface, to prevent them from escaping. According to Hyatt (1979) the branchial arches in fishes are often modified in accordance with the feeding strategy. The sharp spiky gillrakers of the geelbek would presumably also aid in the ingestion of whole live fish as would their large terminal mouths and posteriorly pointed needle-shaped teeth. All prey items obtained from geelbek stomachs were swallowed whole.

Although geelbek are caught during the day, circumstantial evidence suggests that feeding occurs mainly at night. Most geelbek landed in the S.W. Cape and Australia are caught between sunset and sunrise (Roughley 1953, personal communication with

fishermen). Despite the fact that fish are generally more able to avoid nets during the day (Armstrong, SFRI, pers. comm.), Da Franca & Da Costa (1972) found that bottom trawls for geelbek off Angola during the day were much more productive than at night. This would imply that geelbek rise into the pelagic zone during the hours of darkness, where their prey are most likely to be found.

Theoretically the fish would enjoy a number of advantages by hunting at night. The "confusion effect", an anti-predatory mechanism of fish shoals, relies on the fast movement of small flashy fish to hinder the ability of a predator to target on a specific individual (Partridge 1982). The effectiveness of this mechanism would therefore be impaired by reduced light conditions. Furthermore, even with limited illumination, shoals of food near the water surface would be silhouetted when approached by predators from below. The predators on the other hand would be inconspicuous coming from an area of comparative darkness. Evidence for visually based nocturnal feeding comes from Roughley (1953) who stated that A. aequidens bite most freely when the moon is full and not at all if the night is dark.

Munz & McFarland (1973) have found differences in the visual structures of nocturnal and diurnal species of tropical marine fishes. It is therefore possible that in evolving a nocturnal feeding strategy, the eyes of the geelbek would be more adept to lower light intensities than those of its prey.

It would appear that A. aequidens has evolved a specialized feeding strategy which allows it to maximally exploit pelagic shoaling fishes, in particular S. ocellatus and E. capensis. Although the component behavioural and morphological adaptations have precluded the utilization of demersal species, the lipid storage system provides energy during periods of reduced pelagic prey abundance and high energy demand. The relative paucity of reef fishes in the diets of the geelbek is believed to be due to its inability to capture non-schooling prey, or those which do

not maintain shoal formation when attacked. Active prey selection is unlikely as geelbek will accept almost any bait. This conclusion is in agreement with Hughes (1980) who argues that the more specialized a species becomes, the less able it is to handle a wide range of prey.

As a result of the postulated feeding specializations of A. aequidens, one would expect a close association between this species and its prey. Evidence to this effect comes from the previously discussed movements of geelbek in the S.W. Cape in relation to anchovy distribution, and the fact that although adult geelbek spawn in Natal in spring, they first arrive in this region in mid-winter at the same time as S. ocellatus (see Chapter 5). In addition, the arrival of adult geelbek in the Port Alfred area is generally heralded by the occurrence of extensive pilchard shoals (personal observation and communication with fishermen).

It is possible that the intimate relationship between A. aequidens and S. ocellatus may help to further elucidate the migratory pattern of the former species. In Chapter 3 it was shown that during late spring and summer there is a marked reduction in the catches of adult geelbek made by the South African linefishery. It is reasonable to assume that spent fish, having depleted their energy reserves during their migration and for gonad development, are required to feed. During late spring and summer S. ocellatus on the eastern seaboard are most abundant on the Agulhas Bank (Crawford 1981b, Armstrong et al. 1987). It is therefore tenable that after their passive southerly migration (with the Agulhas Current), adult geelbek spend the summer feeding on the Agulhas Bank. They would theoretically remain in this area until autumn when they accompany their prey back to Natal. A possible explanation for the relatively low catches of geelbek made in the S. Cape (Fig. 3) and their poor representation in the spawning migration (Fig. 7) is that the continental shelf runs further out to sea in this region (see Chapter 2). As a result A. aequidens and their prey may become

more dispersed, occurring in lower concentrations and often passing beyond the grounds of the linefishermen. The lack of S. ocellatus in the diets of the sub-adults in the S.W. Cape provides evidence for a spatial separation of mature and immature fish. It also provides an explanation as to why the adults form a negligible component of the geelbek catches made in the S.W. Cape.

As feeding is ultimately concerned with the acquisition of sufficient energy for the completion of the life cycle, the advantages of the feeding strategy of A. aequidens are perhaps best interpreted in terms of energetic requirements. The life history strategy of the geelbek includes a migration as well as the production of relatively large gonads (see Chapters 3 & 5), both of which are energetically expensive (McKeown 1984, Wootton 1985). Pilchards, which were the principal food item of adult geelbek, have also been shown to have a high energy content (Culley 1971). The temporal and spatial migratory pattern of S. ocellatus is also similar to that of the geelbek, thus providing a consistent food supply, which circumvents potential problems associated with qualitative and quantitative changes in available food (McKeown 1984, Townsend & Winfield 1985). A further advantage of a pilchard diet is that during the migration the predator is not restricted to particular substrata for food. It is also likely to encounter prey where migratory conditions such as counter currents or water temperatures are optimal and energetically least expensive.

The feeding strategy of the geelbek is therefore postulated to have evolved as an adaptation to satisfy the energy demands of the reproductive phase of its life history cycle. The development of an extensive energy storage system may be regarded as a physiological adaptation to this end. It is also speculated that the regular occurrence and migration of S. ocellatus on the South African eastern seaboard (Baird 1971, Crawford 1981b) has been of major importance to the evolution of the life history pattern exhibited by A. aequidens.

As revealed by the results of this study, subadult geelbek remain in the S.W. Cape region, where they feed mainly on anchovies until they attain sexual maturity. As a result of their exploiting a different prey population, immature fish firstly do not compete with the adults for energy resources vital for reproduction, and secondly have effectively increased the total amount of available food and hence the carrying capacity of the environment for the population as a whole. In addition, by not undergoing an extensive migration a larger proportion of the ingested energy is available for growth.

From the preceding discussions on feeding, energy storage and gonad development, it might be concluded that food abundance is likely to have been an important controlling factor in unexploited geelbek population levels. Crawford (1987) has presented a considerable body of evidence to show that the performance of marine predator populations are directly dependent on prey availability. The specialized feeding strategy of A. aequidens is therefore expected to render them particularly sensitive to changes in prey abundance, particularly S. ocellatus which provides the energy for gonadal development. It is well established that since the mid-nineteen sixties, mans activities have drastically reduced the pilchard stock in the W. and S.W. Cape (Crawford 1981b). As a direct result Baird (1971) recorded reductions in the intensities of pilchard migrations to Natal.

However, the South African linefishery has reduced the geelbek population to levels far below those of the pristine condition (see Chapter 7). As a result, it cannot be assumed with any reasonable measure of confidence that food remains a limiting factor. Therefore, apart from recognizing the fact that a decline in the South African pelagic fishery has the potential to detrimentally affect the geelbek population, no definite conclusions on this subject are possible.

Nevertheless, it is of relevance to mention that the effects of a

reduced food supply are expected to be enhanced by interspecific competition. Both S. ocellatus and E. capensis contribute substantially to the diets of a diverse range of predatory animals, all of which are encountered on the South African eastern seaboard. These include at least ten species of teleosts (Hecht 1976, Van der Elst 1976, Nepgen 1982, Smale 1985, 1986), the Cape fur seal (David 1987) and numerous species of sea birds (Duffy et al. 1987, Berruti & Colclough 1987), dolphins (G. Ross, Port Elizabeth Museum, pers. comm.) and sharks (J. Cliff, Natal Sharks Board, Umhlanga Rocks, pers. comm., L.J.V. Compagno, J.L.B Smith Institute of Ichthyology, Grahamstown, pers. comm.).

Interspecific competition is also expected to have contributed to the selective pressures favouring the feeding specializations exhibited by A. aequidens.

6.4 Conclusion

The geelbek is a highly specialized marine predator which has become adapted to feed on pelagic shoaling species in order to satisfy the energy demands of the reproductive phase of its life cycle.

The sub-adult fish exist in the S.W. Cape where they feed predominantly on E. capensis. As in the case of the adults, the movements of this sub-population are apparently closely tied to those of their primary food source. The diet of the adults consists mainly of S. ocellatus. Although they utilize this resource throughout their entire spawning migration, they take advantage of a seasonal abundance of pilchards in the S.E. Cape during early winter to accumulate energy reserves for gonadal development. Juveniles of less than one year old, are found in the S.E. Cape where they feed initially on mysids and then on both S. ocellatus and E. capensis.

CHAPTER 7

STOCK ASSESSMENT

7.1 Introduction

Unexploited populations, of any animal group, do not increase indefinitely. They generally reach the carrying capacity (K) of their environment, at which point some factor e.g. food (for adults, juveniles or larvae) becomes limiting. The most commonly observed pattern of population growth is that represented by a logistic curve (Pitcher and Hart 1982). As the population approaches K , density dependent limitations come into play and ultimately ensure a theoretically constant biomass where inputs from population growth equal the outputs due to natural mortality.

The harvesting of such a population would reduce or eliminate the density dependent limitations and once the population returns to K , would theoretically have allowed a net population growth of the magnitude harvested. As illustrated by Figure 37, harvesting regimes affect the rate at which the biomass will grow back to the equilibrium level along the logistic curve. This figure also shows that biomass regeneration occurs at a slower rate along the upper part of the logistic curve, for example, at time B when a smaller crop is taken. From time C a series of regular crops is shown which keeps the biomass oscillating between the levels indicated by the points X and Y. This regime exploits the part of the logistic curve which gives the maximum rate of biomass regeneration. Beyond time D, crops are taken too frequently for the biomass to keep pace and eventually the population is reduced to non-viable levels. At time E, a single large crop has the same effect. In the latter two cases, a negative net population growth is achieved through overfishing. This may occur either as a result of reduced recruitment due to a paucity of spawners (recruitment overfishing), or as a result of declining somatic growth following reductions in the number of growing individuals

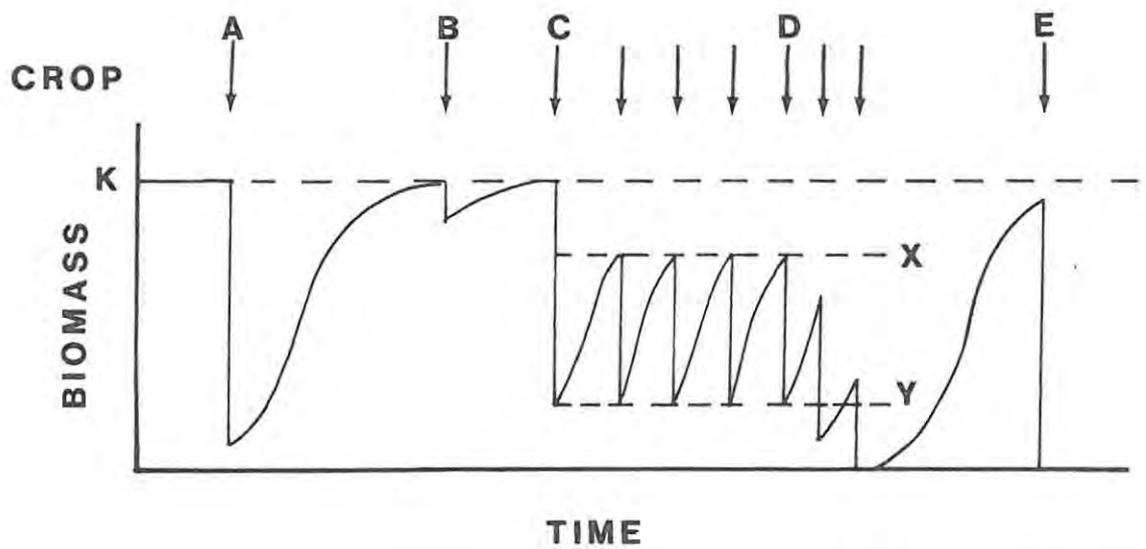


Figure 37. Biomass plotted against time for a cropped population which generates biomass according to a Logistic-type Model (modified from Pitcher & Hart 1982). K represents the carrying capacity. The remaining symbols are explained in the text.

and capture before sufficient growth has occurred (growth overfishing) (Cushing 1981, Gulland 1983).

Although population biomass is a major factor determining the rate of population growth, the age structure of the population also plays an influential role. The reason for this is that the rates of natural mortality and somatic growth of the fish within a population depend on their age (Nikolskii 1969, Royce 1972, Ricker 1977, Pitcher and Hart 1982). In younger age groups weight increases due to somatic growth usually outweigh losses due to natural mortality, with the result that the respective cohorts would display positive growth in the absence of fishing (Cushing 1981). It therefore follows that optimal population growth rates will be achieved by manipulating the fishing effort (and hence the biomass) as well as the age at first capture.

Numerous mathematical models have been developed in attempts to calculate optimal fishing levels on fish populations. These may be divided into two groups. The first group includes the production or surplus yield models of which the Shaefer (1954) model is a classic example. These models are based on time series of catch and effort data. However, they unfortunately do not consider the events that occur within a population, in particular growth and mortality of the individuals forming that population.

The analytic or dynamic pool models (e.g. the Beverton and Holt (1957) yield per recruit model) comprise the second group. Incorporated in these models are two improvements which theoretically impart greater realism to fisheries management. Firstly, the separate processes which alter fish population biomass are described explicitly as components of the model. Secondly, the age structure of the population is included.

In this study the condition of the South African east coast geelbek population was assessed using yield per recruit and spawner biomass per recruit models, both of which belong to the

dynamic pool group. Unlike the widely used Beverton and Holt model, the yield per recruit equation used in this investigation was completely general and did not specify the shape of the yield contour surface in advance (Pitcher & Hart 1982). Furthermore, instead of using a single mortality rate for the entire population, the model utilized age specific mortality rates. This is important when dealing with migratory species, such as A. aequidens, where different age groups within a population may be found in different areas and therefore have different rates of exploitation.

A disadvantage of yield per recruit models is that they pay no attention to the consequences of the distribution of effort on a population (M. Armstrong, SFRI, Cape Town, pers. comm.). For example, although a population as a whole may be fished at an optimal mortality rate (according to a yield per recruit model), higher rates in the spawner stock may reduce this group to levels where recruitment is detrimentally affected. Geelbek undergo a spawning migration throughout which they are vulnerable to capture. In addition the cohort analysis described in this chapter revealed that the mature fish were exposed to higher rates of exploitation than those that were immature. A spawner biomass per recruit curve was therefore generated for the geelbek using a model developed by Armstrong (pers. comm.).

Size limits are often based on lengths at 50% sexual maturity, so that fish are given at least one chance to breed (Buxton 1987). This rationale is, however, impractical in the case of the geelbek as 50% sexual maturity is only attained at 900 mm FL (953 mm TL), and hence would exclude most of the fish presently caught in the S.W. Cape and a large proportion captured in the S.E. Cape (see Fig. 5). On the other hand the arbitrarily determined size limit of 400 mm TL (378 mm FL) in the Cape Province and 400 mm FL in Natal (Van der Elst 1981, Anon. 1984) creates the unsatisfactory condition where the fish are exploited before they have had a birthday. This clearly illustrates the need for a more scientifically based size limit for A. aequidens.

An attempt was therefore made to calculate an optimum age at first capture by investigating the effects of the interplay between natural mortality and somatic growth on the biomass of a cohort.

7.2 Material

Basically two types of data were used to complete the current investigation. These included the 1986 regional length frequencies presented in Chapter 3 and values for the annual catches of A. aequidens made during that year by commercial fishermen in each region along the South African east coast (Linefish Data Base, SFRI, Cape Town). The reason why only the 1986 data were used was that data collection was terminated before the end of 1987 and, as previously mentioned, the length measurements for 1985 were not entirely random.

7.3 Methods and Results

Age Composition of the 1986 Catch

This section is concerned with the calculation of an age frequency distribution in terms of absolute numbers which is representative of the entire catch of geelbek made along the South African eastern seaboard during 1986.

According to Van der Elst (ORI, Durban, pers. comm.) recreational fishermen catch approximately 15 per cent of the total landings of geelbek in Natal. Similar estimates were obtained for both the S.E. and S.W. Cape by comparing dealer returns (from the Linefish Data Base) with those of commercial fishermen. The established differences are not considered to be due to under reporting by the commercial fishermen (C. Wilke, SFRI, Cape Town, pers. comm. and personal observations).

By comparing the gutted and whole weight of 800 geelbek (270-1040

mm FL) it was established that the viscera make up approximately 11% of the total weight of fish. Using this correction factor the SFRI catch statistics were adjusted to produce estimates of total catch weight for the respective regions. Also accounted for were the catches made by recreational fishermen.

Because very few length measurements were obtained from the S. Cape and none from the Transkei (see Chapter 2) the 1986 SFRI catch figures for these two regions were added to and processed with those of the S.E. Cape and Natal respectively. Communication with fishermen and Sea Fisheries inspectors indicated that the length frequencies of A. aequidens from each of the former two regions were similar to those with which their catch figures were combined.

Raising factors were calculated by dividing the estimated total catches from each region by the total weights of the fish measured in the respective regions. The weights of the sampled fish were calculated by using the length weight relationship (see Chapter 4) and the regional length frequencies.

The sampled length frequencies for the three regions (S.W. Cape, S.E. Cape and Natal) were multiplied by their respective raising factors to calculate the absolute numbers per length class in the total catches. The numbers per size class in each of the three regions were simply added to obtain a length frequency distribution, in terms of absolute numbers, for the entire South African 1986 catch. This length frequency distribution was converted to an age frequency distribution (see Table 11) by normalization and matrix multiplication using the age length key constructed in Chapter 4.

Table 11. The age frequency distribution in terms of absolute numbers of Atractoscion aequidens caught along the South African eastern seaboard during 1986.

AGE (t) (years)	NUMBERS (N)
0	7513
1	20343
2	21536
3	6900
4	7719
5	5491
6	1717
7	527
8	164

Calculation of Instantaneous Rates of Natural (M) and Fishing (F) Mortality

In this section an instantaneous rate of fishing mortality (F) was calculated for the oldest age groups, as a starting point for the calculation of age related mortality rates as described in the next section.

Since mature geelbek of all age classes shoal together it is logical to assume that they have similar rates of total mortality (Z). An estimate of Z for fish of six years (age at 100% sexual maturity) and older was obtained by constructing a catch curve (Fig. 38) (see Ricker 1975, Gulland 1983) where:

$$Z = - (\text{slope}) = 1,21$$

Instantaneous natural mortality was calculated using Pauly's (1980) equation:

$$\log_{10}M = -0,0066 - 0,279 \log_{10}L_{\infty} + 0,6543 \log_{10}K + 0,4634 \log_{10}T$$

where M = instantaneous rate of natural mortality

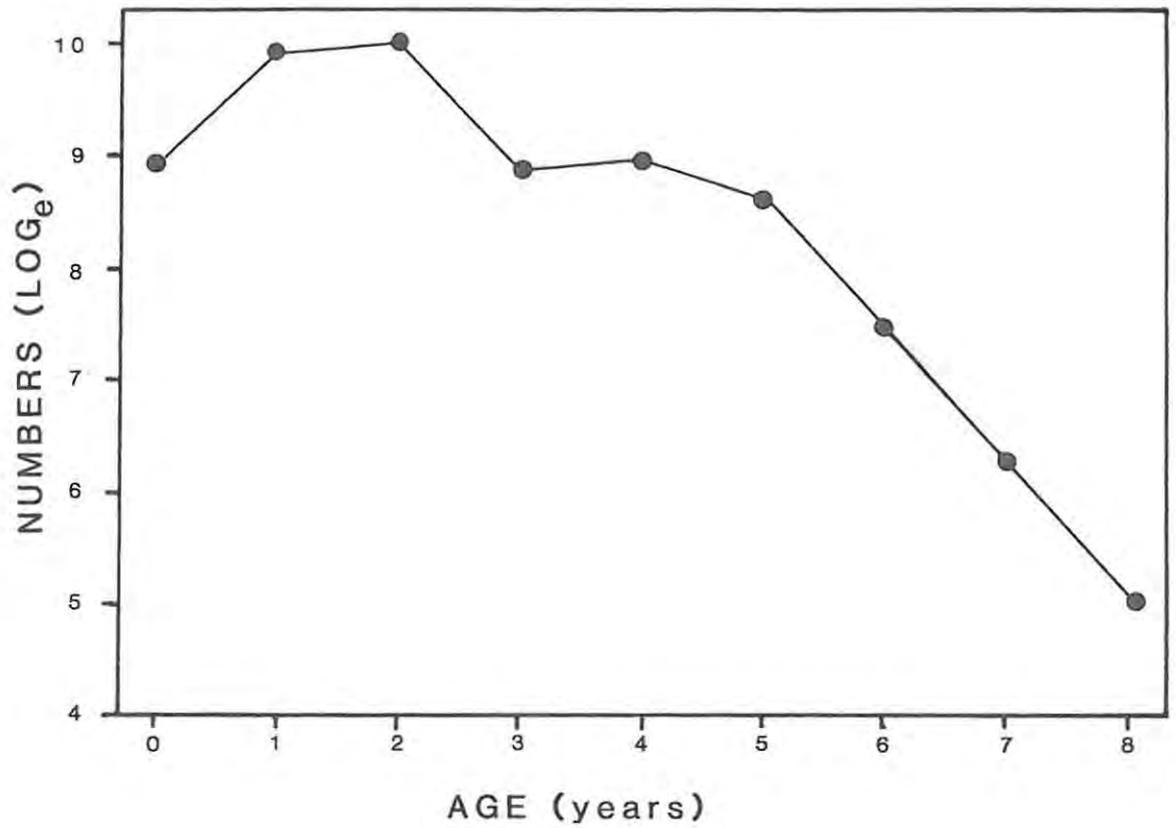


Figure 38. Catch curve for *Atractoscion aequidens* off the South African eastern seaboard, 1986.

L_{∞} = the theoretical asymptotic length (cm) of A.aequidens from the von Bertalanffy growth equation (see Chapter 4).

K = the von Bertalanffy growth coefficient

T = the mean annual temperature ($^{\circ}$ C)

A mean temperature value of 20° C was used. This value is based on bottom temperature readings obtained from the South African Data Centre for Oceanography (SADCO) in Stellenbosch. The readings used were recorded from several localities along the east coast at suitable depths. Natural mortality was calculated to be $M = 0.41$.

Using the relationship $Z = F+M$, fishing mortality for fish older than five years was calculated at $F = 0,8$.

Calculation of Age Related Instantaneous Fishing Mortalities (F_t)

In order to calculate age related rates of fishing mortality Pope's (1972) method of cohort analysis was followed as described by Jones (1984). This method is a simple approximation of Virtual Population Analysis (Jones op. cit.). It was developed to allow VPA equations which originally contained too many unknowns, to be solved. Popes method also required that $F > M$, a condition which definitely appears to be met in the case of geelbek.

According to this method the numbers attaining the oldest age group in the geelbek population were calculated by:

$$N_t = \frac{C_t}{F(1-e^{-Z})/Z} \quad (\text{Jones 1984})$$

N_t = numbers at age

C_t = catch at age

F = instantaneous rate of fishing mortality

Z = total mortality

The oldest age group was taken to be seven years because very low numbers of fish of eight years and older were captured. The reason for the exclusion of the oldest age groups was that possible inaccuracies due to misrepresentation (as a result of low sample numbers), would have been transmitted to the values for the younger age groups by subsequent calculations.

Successive values of N_t for the younger age groups were calculated from:

$$N_t = (N_{t+1}e^{M/2} + C_t)e^{M/2} \quad (\text{Jones 1984})$$

Age specific total instantaneous mortality rates (Z_t) were calculated from the relationship between the survival rate (S_t) and Z_t :

$$S_t = e^{-Z_t} \quad (\text{Jones 1984})$$

and therefore $Z_t = -\ln S_t$

Values of F for each age interval (F_t) were then simply determined from the equation:

$$F_t = Z_t - M$$

Based on the assumption that fish of six years (age at 100 per cent maturity) and older should have equal values of F_t , iterative procedure was followed by completing the cohort analysis using alternative initial estimates of F. The resulting F_t values failed to satisfy the above criterion. The F_t values obtained by cohort analysis initially using $F = 0.8$ were therefore accepted. They are illustrated in Table 12.

Table 12. The age related fishing mortality rates (F_t) as generated by Pope's (1972) method of cohort analysis.

Age (Years)	F_t
0	0,034
1	0,153
2	0,302
3	0,185
4	0,413
5	0,785
6	0,808
7	0,80

The higher rates of fishing mortality associated with geelbek above the age at 100% maturity (6 years) (Table 12) are believed to be due to the inshore spawning migration of this species where they are highly vulnerable to fishing. Table 12, however, shows that the five year olds also had a relatively high rate of F . The most probable reason for this observation is that while 50% of this age group are mature and are expected to migrate to Natal, there are a substantial number of "adolescents" (Chapter 5) which undergo a partial migration to at least as far as the S.E. Cape, and would therefore experience similar rates of exploitation as the adults.

Yield per Recruit

A modern dynamic pool model, built around the summation of yields for each age class was used to generate a yield per recruit (Y/R) curve. The equation used was:

$$Y/R = \sum_{i=t_r}^4 \left\{ \left[\frac{F_i}{F_i + M} \right] (1 - \exp(-(F_i + M))) (\exp(-\sum_{j=t_r}^i F_j + M)) \bar{W}_i \right\} \quad (\text{Pitcher \& Hart 1982})$$

t_l = maximum age of fish in stock
 t_r = age at recruitment to fishable stock
 \bar{W}_i = mean weight at age
 F_i = instantaneous fishing mortality at age
 M = instantaneous natural mortality

The pattern of selectivity observed by the variable F_t values in Table 12 was retained when substituting alternative sets of F_t values to calculate respective yields. The yield per recruit curve is shown in Figure 38. The mortality rates on the abscissa refer to the maximum F_t values of each alternative set of F_t used.

Yield per recruit curves may take on a number of forms (Beverton & Holt 1957, Cushing & Bridger 1966, Hughes 1986). In cases where they form a distinct asymptote, the F value associated with the maximum yield per recruit is generally accepted as the management objective (Beverton & Holt 1957, Gulland 1983, Hughes 1986). However, in cases such as Figure 39, where the curve does not display asymptotic behaviour, the $F_{0,1}$ value has become a widely accepted management goal (Gulland 1983, Hughes 1986, Andrew & Butterworth 1987). This may be defined as the F value corresponding to a point on the yield per recruit curve where the slope has been reduced to 10% of its initial value. The $F_{0,1}$ value calculated for the geelbek yield per recruit curve was found to be $F_{0,1}=0,6$ (see Figure 39).

Spawner Biomass per Recruit

A spawner biomass per recruit (SB/R) curve was constructed for A.aequidens using the following equation:

$$SB/R = \sum_{i=t_s}^{t_l} \left\{ \exp\left(-\sum_{j=t_r}^{i-1} (F_j+M)\right) \bar{W}_i \right\} \quad \text{(M. Armstrong, SFRI, Cape Town, pers. comm.)}$$

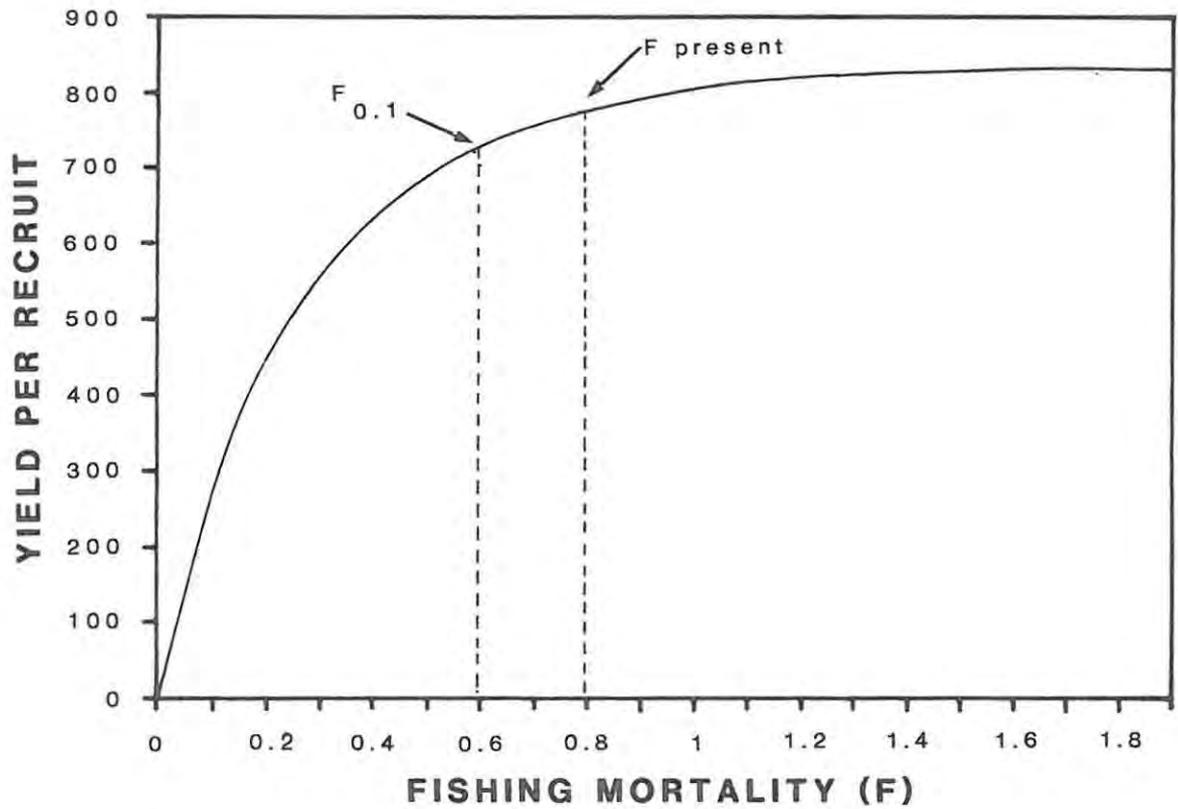


Figure 39. The yield per recruit curve for Atractoscion aequidens off the South African eastern seaboard. The $F_{0.1}$ value and present level of fishing mortality (F_{present}) are both indicated.

t_s = age at 50% maturity

This relationship is represented graphically in Figure 40.

According to Shaefer (1954) the biomass of a population, which displays logistic growth, should optimally be maintained at 50% of the carrying capacity or unexploited condition ($0,5K$). This rationale may be extended to the biomass of the spawner stock. Clark *et al.* (1985) and Bergh and Butterworth (1987) have assumed that recruitment will be detrimentally affected if the spawner biomass of fish populations is allowed to fall below the $0,2K$ mark. This somewhat arbitrary assumption is also widely used by the Pelagic Division of the South African Sea Fisheries Research Institute (Armstrong, pers. comm.).

The spawner biomass per recruit and fishing mortality values corresponding to the $0,2K$, $0,5K$ and present biomass levels are all indicated in Figure 40.

Optimum Size Limit

The individuals comprising a cohort in an unexploited population will decrease in number due to natural mortality at the same time as they increase in weight due to somatic growth. In an exploited situation it would be logical to begin capturing fish at an age at which the positive growth of the cohort biomass begins to slow down.

A theoretical unexploited cohort biomass growth curve was constructed (Fig 41). Numbers-at-age were calculated by decaying the number of recruits generated by the cohort analysis by the previously estimated rate of natural mortality. The von Bertalanffy equation expressing growth in terms of weight was then used to calculate biomass-at-age.

Figure 41 shows that the biomass of an unexploited geelbek cohort would increase rapidly in its first two years. A much slower

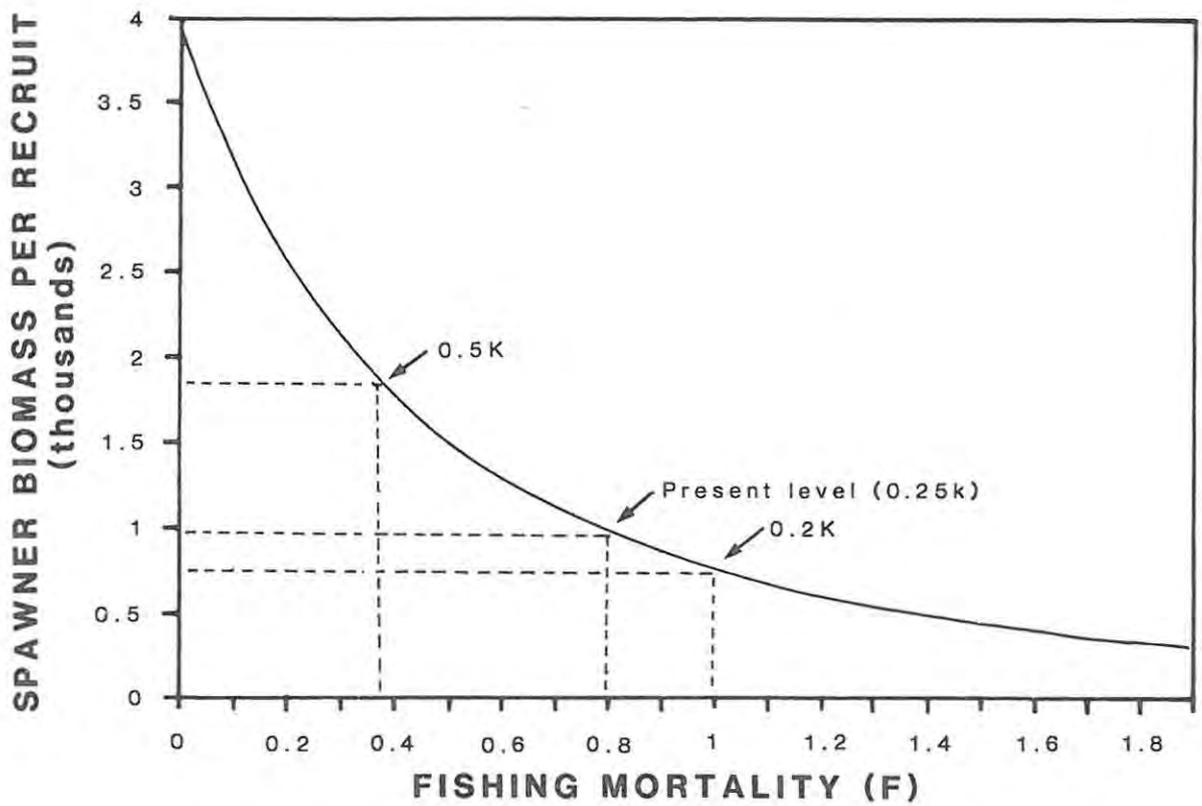


Figure 40. The spawner biomass per recruit curve for Atractoscion aequidens along the South African eastern seaboard. The various points on the curve are explained in the text.

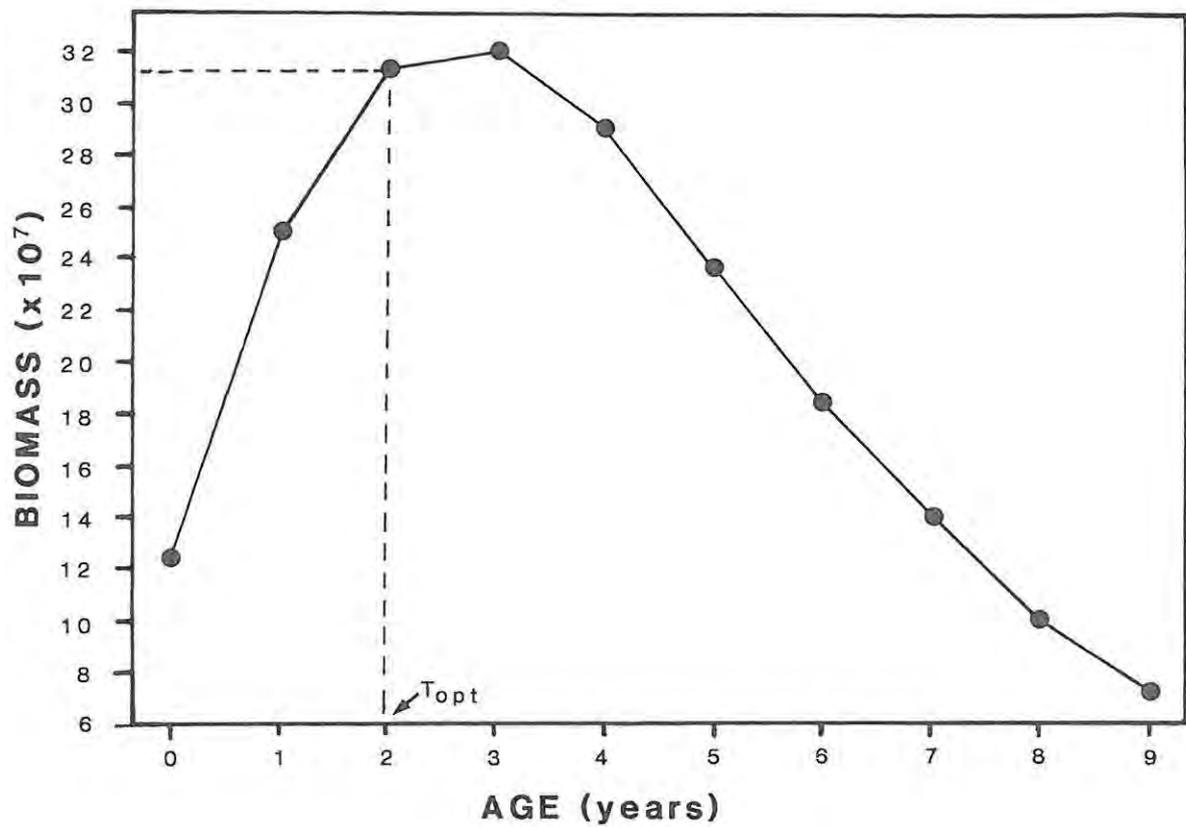


Figure 41. The theoretical growth of an unexploited Atractoscion aequidens population. T_{opt} indicates the optimal age at first capture.

rate of increase was observed from ages two to three, after which the biomass declines rapidly. Although the cohort biomass reaches a peak at age three, the rate of biomass decline between ages three and four was much higher than the rate of increase from ages two to three. Therefore, to reduce the biomass loss due to natural mortality and to increase the landed weight of a particular cohort, it was assumed to be logical that the optimum age at first capture should be two years. This corresponds to a fork length of 660 mm and a total length of 700 mm.

7.4 Discussion

Ricker (1975) stated that in using an age length key for stock assessment, the fish used for age determination must be taken from the same stock, during the same season of the same year and using gear having the same selective properties as that used to take the length frequency samples. Unfortunately these criteria were not met on all accounts during this study. To obtain age representation for all lengths it was necessary to sample fish from the S.W.Cape, the S.E.Cape and Natal. Due to the migratory nature of the geelbek, aging material was obtained during different seasons in the three regions. Although the material from Natal and the S.W.Cape was collected during 1986 some of the material from the S.E.Cape was collected during 1985. These otoliths, however, only comprised 37% of the total number used for aging. Furthermore, compared to many exploited pelagic fishes, the geelbek is a relatively long lived species. It was therefore reasonable to assume that the lengths of older fish would be a result of both "good" and "bad" growth years. Consequently one would expect less annual variation in the lengths-at-age of this species than in those which are shorter lived, and on which Ricker's statement might have been based.

VPA and cohort analysis were originally developed to calculate fishing mortality rates based on the differences in the numbers from particular cohorts as these passed from one year to the next (Pitcher & Hart 1982, Gulland 1983, Jones 1984). To carry out

cohort analysis on one years data, it had to be assumed that the population was in an equilibrium condition and that numbers found in respective year classes were equivalent to the average annual numbers in these respective year classes. Such a state of dynamic equilibrium is unlikely to exist in an exploited population where variable rates of both recruitment and fishing mortality are expected to cause the numbers in the different year classes to deviate from the ideal. Unfortunately there was no way of assessing how closely the calculated mortality rates in this study approached reality. For this reason the assessment of the geelbek stock based on both the yield per recruit and spawner biomass per recruit curves should only be regarded as being of a preliminary nature. The construction of yield isopleth diagrams and the simulation of the effects of varying fishing mortality and age at first capture were therefore not undertaken.

A further potential source of error arises from the occurrence of geelbek in southern Mozambique (Fischer & Bianchi, 1984). No information was available on the relative abundance of geelbek in this area. Abundance was not expected to be high as the coastal waters of this region are strictly tropical and hence very different from those off South Africa (Christensen 1980, Branch & Branch 1983). However, if significant catches of geelbek are in fact made in Mozambique, and assuming they belonged to the same stock, then their exclusion from the calculations would have resulted in artificially high estimates of fishing mortality.

An additional assumption, which may affect both the stock assessment and the optimal size at first capture, was that natural mortality was taken as being constant for all ages. Although this may not be realistic (Nikolskii 1969, Pitcher & Hart 1982, Gulland 1983), the latter two authors have pointed out that in most cases the determination of age related rates of natural mortality are impossible.

Despite the preceding comments, Figures 39 and 40 indicate that A. aequidens is fished at F values above the $F_{0,1}$ level and that

the spawner biomass at 0,25K is closely approaching the critical 0,2K level. It should, however, be remembered that the latter criterion was derived completely arbitrarily. It is therefore possible that recruitment would begin to be reduced at a higher spawner biomass (e.g. 0,3K). Further examination of Figure 40 shows that the optimal level of 0,5K is achieved at $F=0,36$, which is less than half of the current value of $F=0,8$.

From this preliminary investigation it could be concluded that the geelbek population is presently overfished and in a potentially dangerous position, with the possibility of recruitment overfishing occurring in the near future. The migratory nature of the geelbek is in all probability a contributing factor to the condition of the stock as this phenomenon has led to high rates of fishing mortality in the relatively few year classes of adult fish (see Table 12). A very real need therefore exists for additional information to undertake a more accurate assessment of the stock of this important species. This information should include comprehensive length measurements for at least three years to achieve more confident age related rates of fishing mortality. Attempts should also be made to obtain length measurements from the S.Cape and Transkei, and to obtain an indication of the catches and the catch composition of the species in Mozambique. Management alternatives could then be simulated using dynamic pool models, in order to establish the optimal combination of size at first capture and fishing mortality.

Nevertheless, in the section entitled "Optimal Size Limit", evidence was presented to suggest that the age and size at first capture should be increased to 2 years and 700 mm TL (660 mm FL) respectively. Based on the regional length frequencies (Chapter 3) and the length-weight relationship, an increase of this magnitude would exclude 33% of the present catch by weight in the S.W. Cape, 16% of the catches in the S.E. Cape and essentially nothing from the catches in Natal. The excluded fish, however, would belong to cohorts undergoing rapid positive growth.

Consequently, future returns could be expected to be increased by percentages far greater than those due to losses initially incurred by the imposition of such a legal size limit.

CHAPTER 8

FINAL DISCUSSION AND CONCLUSIONS

From the preceding results and discussions it was concluded that the South African geelbek population comprises a single stock and therefore should be managed as such. As is common amongst oceanodromous migratory species (Harden-Jones 1968, McKeown 1984), this stock is divided into three age-related sub-populations.

Immature or sub-adult fish (1-4 years) occur mainly in the S.W. Cape where they feed predominantly on E. capensis. The movements of this sub-population are closely linked to those of their prey. During summer they are concentrated inshore but it was postulated that they move out over the eastern Agulhas Bank in winter.

On attaining sexual maturity these fish join the adult sub-population (5-9+ years) which undertakes an inshore migration to Natal where they spawn offshore in the Agulhas Current during spring. The migration occurs in close association with that of S. ocellatus, their major food source. As a result, both species arrive in Natal in mid-winter. After spawning it is hypothesised that the geelbek remain offshore and "ride" the current southwards to the Agulhas Bank where they spend the summer feeding on an abundance of pilchards. In autumn both predator and prey begin the north eastward migration back to Natal, thus completing the cycle. There is also evidence to suggest that adolescent fish (4/5 years old) undertake a partial migration together with the adults to at least as far as the S.E. Cape. Their subsequent movements are, however, unknown.

It was postulated that the eggs and larvae are carried southwards from the spawning area on the edge of the Agulhas Current. After metamorphosis the juvenile fish move inshore where they are recruited to the linefishery in the S.E. and possibly S. Cape. They are initially planktivorous, feeding predominantly on

mysids, but later become piscivorous, consuming both pilchards and anchovy. Although the S.E. Cape appears to be a nursery area for the juveniles, they gradually move westwards to the S.W. Cape where they remain until they begin to attain sexual maturity. Figure 42 summarizes the life history cycle of this species.

In evolving this life history strategy, the geelbek has become adapted to regular patterns in both the biotic (prey movements) and the abiotic (Agulhas Current) environment. The component adaptations include: a specialized feeding strategy; the development of an extensive energy storage system; fast growth and late sexual maturity; and an upcurrent spawning migration coupled with a pelagic spawning tactic.

As a result of its relatively late age at sexual maturity, the inshore and longshore migration of reproductively mature fish and a voracious feeding behaviour, this species is particularly vulnerable to overexploitation. Evidence from an albeit preliminary stock assessment indicated that the geelbek population is already fished above optimal levels of exploitation. It is therefore essential that appropriate management strategies be implemented if this highly prized linefish is to be maintained as an important component of the South African linefishery.

The South African linefishery can broadly be divided into commercial and recreational sectors. Legislation passed in 1984 (Anon. 1984) has limited the geelbek catches of recreational fishermen to 10 fish per man per day. However, as was shown in Chapter 7 this user group only contributes approximately 15% to the total annual geelbek catch. It is therefore also necessary to limit the catches of the commercial fisherman.

A combination of the multispecies nature of the South African linefishery and the effects of barotrauma generally present a problem to the implementation of both bag and size limits to many species within the fishery (Garrat 1984, Buxton 1987). To be more explicit, many undersized fish, or those accidentally caught

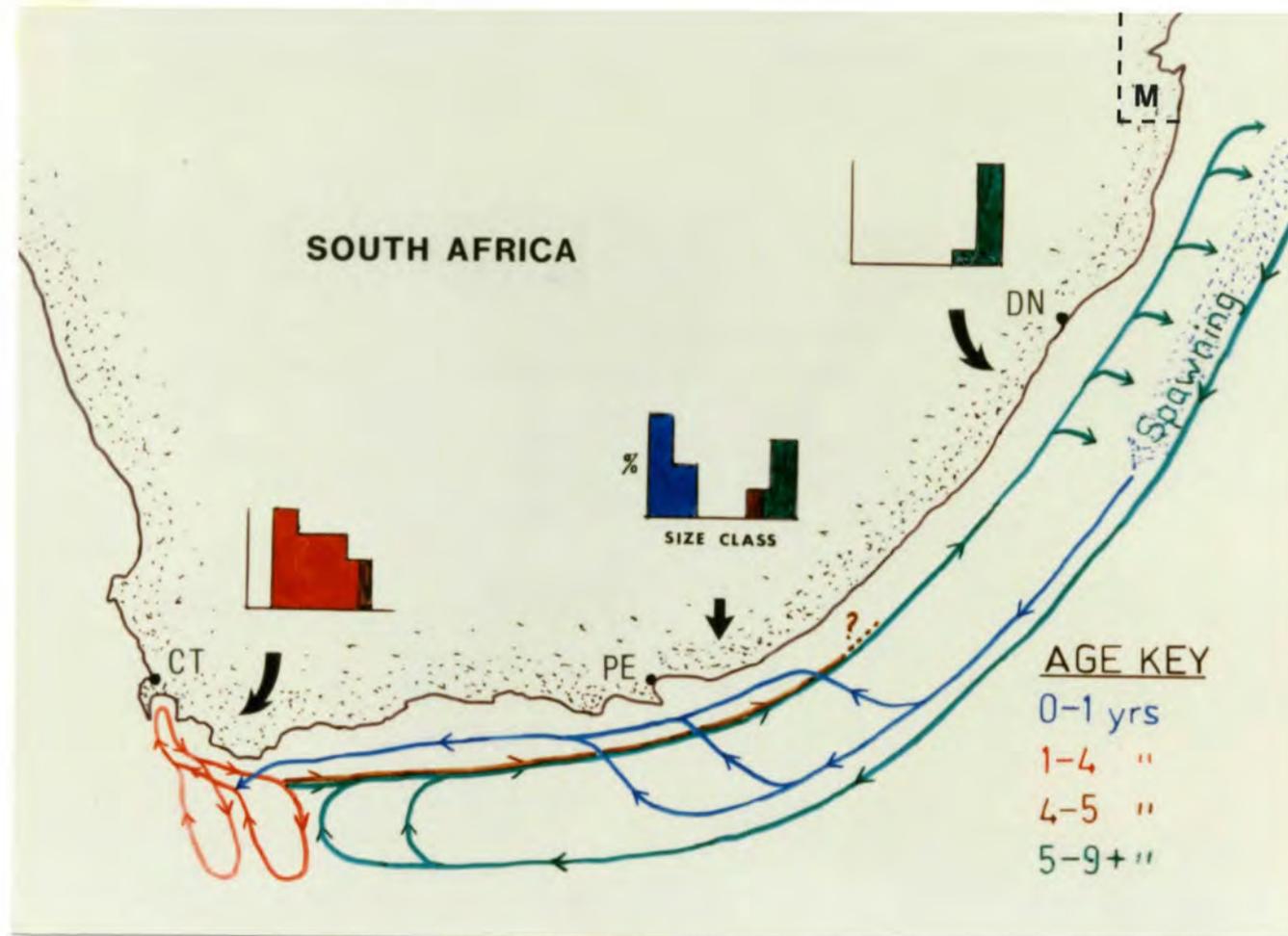


Figure 42. The theoretical life history cycle and migratory patterns of the various age-related sub-populations of *Atractoscion aequidens* along the South African eastern seaboard. For the sake of clarity, the lateral dynamics of the migratory patterns are not drawn to scale. M = Mozambique, DN = Durban, PE = Port Elizabeth and CT = Cape Town. For further geographic localities and oceanographic features see Figure 2 (Chapter 2).

in excess of species specific quotas, will die even if they are immediately returned to the water after capture. Geelbek, however, generally form concentrated shoals of equal sized fish which are often targeted for on specific grounds. It is therefore possible for fishermen to move away from such an area once quotas have been filled or if the captured fish do not satisfy the size limit. Consequently, both bag and size limits are particularly appropriate strategies for the management of this species.

Until sufficient data is collected and analysed to enable a more accurate stock assessment, it is suggested that the size limit for A. aequidens be increased from 400 mm TL in the Cape, and 400 mm FL in Natal, to 700 mm TL (660 mm FL) along the entire South African coast. It is also recommended that a bag limit of 5 fish per man per day be imposed on all participants in the South African linefishery.

Although both of these management strategies would have the desired effect of decreasing effort on the geelbek population, this size limit, as determined by investigating the interplay between somatic growth and mortality on an unexploited cohort, was also designed to increase the rate of biomass regeneration for the population as a whole. The combination of reduced fishing pressure, and an increased rate of population growth, would conceivably allow the geelbek population to return to levels which are more acceptable than those indicated by the preliminary population assessment. It is however also advisable that the condition the geelbek population be assessed on a regular basis so that the management strategies can be quantitatively adjusted to maintain the rates of fishing mortality at near optimal levels.

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APPENDIX

Future Research

Although the present study has provided a general understanding of the biology and population dynamics of the geelbek, there are a number of areas where further research could improve the accuracy of this knowledge. These include:

- a) The collection of additional length and age data from fish older than six years, in order to obtain a better fit of the VBG model using the more advanced curve fitting procedures described by Hughes (1986).
- b) Experimental fishing on the Agulhas Bank to test the hypotheses concerning the locality of the 1-4 year olds during winter and the adults during summer.
- c) The collection of monthly length measurements from the S. and S.W. Cape to more accurately define the temporal and spatial movements of all three age related sub-populations i.e. the 0-1, the 1-4 and the 5-9+ years.
- d) Egg and larval surveys in Natal to further delimit the time (daily and seasonally) and the area of spawning.