ASPECTS OF THE BIOLOGY, ECOLOGY AND POPULATION DYNAMICS OF *GALEICHTHYS FELICEPS* (VALENCIENNES) AND *G. ATER* (CASTELNAU) (PISCES: ARIIDAE) OFF THE SOUTH-EAST COAST OF SOUTH AFRICA

THESIS

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ABSTRACT

This thesis represents a detailed investigation into aspects of the biology, ecology and population dynamics of two endemic ariid species, Galeichthys feliceps and G. ater, off the south-east coast of South Africa.

The two species are exploited as a by-catch in the commercial ski-boat fishery off Port Alfred, a fishery dominated by highly fecund sparid and sciaenid species. They collectively constitute approximately 10% of the total annual catch in terms of landed mass. G. feliceps outnumber G. ater in the catches by a ratio of 3:1. The investigation was designed to provide the biological data required for stock assessment and to determine optimum management strategies for the two populations. The implications of their K-selected life-history styles for exploitation received particular attention.

While the two species were sympatric and had similar depth distributions they were found to be allopatric with respect to their foraging habitats. G. feliceps foraged over sandy and muddy substrata in marine and estuarine environments. G. ater fed only on reef-associated species and did not utilise estuaries. Their feeding-associated morphologies were identical and both species preyed primarily on crustaceans (brachyuran crabs and isopods), echiurids, molluscs and polychaetes. The diet of G. ater was broader in terms of the number of species consumed.

The two species are mouth-brooders with low fecundity. G. feliceps and G. ater produced a mean of 49 and 32 eggs each, per annum. The buccal incubation period was determined to be in the region of 140 days for G. feliceps. Embryos hatched after approximately 75 - 80 days and the young began exogenous feeding thereafter. The young fed intra-buccally on detritus provided by the parent. Adult buccal mucus may also have been

used as a food source. Young were released at a total length of ± 55mm. Adult males ceased feeding whilst mouth-brooding. Body musculature, abdominal fat and liver reserves provided energy for basal metabolism and males lost approximately 28% of their body mass during buccal incubation. Females expended less reproductive energy than males.

Catches were dominated by mature fish (76% in G. feliceps and 97% in G. ater). Females were significantly more abundant in catches during the spawning and mouth-brooding period. The female to male sex ratios were 1.65:1 and 2.23:1 for G. feliceps and G. ater respectively.

Age and growth studies revealed that the two species mature at advanced ages (10 and 9 years for G. feliceps and 9 and 7 years for G. ater males and females respectively). They are long-lived, reaching ages in excess of 18 years in G. feliceps and in excess of 15 years in G. ater. Females live longer than males and grow larger. Yield-per-recruit and spawner biomass-per-recruit analyses demonstrated that G. ater were exploited below $F_{0.1}$ at a level where spawner biomass-per-recruit was reduced to between 45% and 65% of the unexploited level. The G. ater stock was not adversely affected by current levels of fishing effort. For G. feliceps, both sexes were exploited beyond $F_{0.1}$ where spawner biomass-per-recruit was reduced to between 30% and 22% of the unexploited level.

G. feliceps were shown to be sensitive to relatively low levels of exploitation, a phenomenon attributed to their highly K-selected life-history style. Should the species become targeted for in the future, effort restrictions in the form of a closed season during the spawning and mouth-brooding period would prove effective in reducing effort and conserving the population sex ratio.

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CHAPTER 1 - INTRODUCTION

Fishes of the family Ariidae are predominantly marine and occur circum-globally in shallow coastal waters of tropical, sub-tropical and temperate oceans. Several species are also estuarine and some penetrate the mid- and upper reaches of rivers where they may live and reproduce in fresh water (Rimmer & Merrick 1983). It is a speciose family, comprising over 150 species (Rimmer & Merrick op cit.), many of which form an important component of both artisinal and commercial fisheries in many tropical and sub-tropical regions of the world (Singh & Rege 1968; Tobor 1969; Wongratana et al. 1974; Dmitrenko 1975; Taylor & Menezes 1977; Etchevers 1978; Jayaram & Dhanze 1978; Warburton 1978; Silas et al. 1980; Dan 1981; Taylor & Van Dyke 1981; Jayaram & Kailola 1983; Muncy & Wingo 1983; Cortés 1984; Menon 1984; Reis 1986; Bawazeer 1987; Brothers & Mathews 1987; Euzen 1987; Coates 1988; Pauly & Thia-Eng 1988).

The siluriformes are thought to have evolved in fresh water in the South American and African tropics (Greenwood et al. 1966), although Roberts (1973) has suggested that they arose independently in Africa, Asia and South America. While the Ariidae are predominantly a marine family, there is evidence to suggest that they also evolved in fresh water (Lundberg 1975a in Grande & Lundberg 1988). While the area of greatest ariid radiation appears to be the Indo-Pacific Archipelago (Wongratana et al. 1974), much of their present day distribution is probably attributable to secondary radiation which would have been facilitated by their marine habit.

Relatively little is known about the evolutionary status of the Ariidae and it has been suggested that they lie at the base of siluroid evolution along with the Diplomystidae (Regan 1911; Shelden 1937; Gosline 1944 in Hassur 1970; Alexander 1965). More recent studies have demonstrated that

they have attained an advanced form and that approximately half of all catfish families are more generalised than the ariids (Tilak 1965; Greenwood et al. 1966; Hassur 1970). Phylogenetic relationships of siluroid fishes have traditionally been based on skeletal structures such as cranial morphology, the Weberian apparatus and the associated swim-bladder, the pectoral girdle and pelvic girdle and the caudal fin skeleton (e.g. Shelden 1937; Alexander 1965; Tilak 1965, 1971; Chardon 1968; Jayaram & Singh 1984; Howes 1985; Grande & Lundberg 1988). The results of these studies have, however, been inconsistent and largely inconclusive. Recent karyological studies (LeGrande 1980, 1981; Fitzsimons et al. 1988) concur with Gosline's (1975) findings (which are based largely on osteology), that the Ariidae, along with the Bagridae, Doradidae, Ictaluridae and Pimelodidae, form a group which reflects the ancestral condition from which living catfishes evolved. They do stress, however, that their interpretations of the karyological data are largely speculative, and their conclusions tentative. Gosline (1975) has argued that the high incidence of parallel evolution within the siluroid group will foil any attempts to accurately reconstruct catfish phylogeny.

Striking features common to all ariids are their mouth-brooding habit and extremely low fecundity (Rimmer & Merrick op. cit.), while the size of their eggs is unsurpassed amongst the teleosts. These reproductive characteristics would place them near the K, or precocial extreme, of the r/K (MacArthur & Wilson 1967) or altricial/precocial (Balon 1979) life-history style continua. This study of two ariid species occurring along the South African south-east coast therefore provided an opportunity to test, amongst other hypotheses, the predictability of the life-history model assumptions with respect to biological traits associated with K-strategist or precocial animals (slow growth, longevity, large average body size, low natural mortality

and vulnerability to sources of unnatural mortality such as fishing), (Adams 1980).

The two South African ariid species, Galeichthys feliceps Valenciennes and G. ater Castelnau are endemic to the coasts of South Africa and Namibia where they frequent shallow coastal waters down to a depth of approximately 60 meters. The colloquial common name for both species is barbel, although G. ater, because of its muddy colouration, is also known as "vuiljassie" (= dirty jacket). The existing distributional records for the two species in the literature are somewhat inaccurate. Taylor (in Smith & Heemstra 1986, p.213) records the distribution of G. feliceps as 'Sea, estuaries and rivers from Walvis Bay to Natal'. The distribution of G. feliceps in rivers is restricted by their intolerance of salinities below 8ppt. (Whitfield et al. 1981; Bennett 1985). The barbel occurring off the coasts of Transkei and Natal grow to a large size and do not enter estuaries, and it is thought that they may represent a distinct Galeichthys species (P. C. Heemstra, JLB Smith Institute of Ichthyology, pers. comm.). The true eastern limit of G. feliceps distribution therefore appears to be in the vicinity of East London. The distribution of Galeichthys ater is recorded as 'South coast to Port Alfred' (Taylor op. cit. p.212), although specimens have recently been collected off the Namibian coast as far north as Swakopmund (pers. obs.). Galeichthys ater and G. feliceps appear to share a similar distribution between Swakopmund in the west and East London in the east. Estuaries play an important role in the life-cycle of G. feliceps, while G. ater are exclusively marine.

The two species have previously been known under three generic names, Arius Valenciennes, Galeichthys Cuvier and Valenciennes, and Tachysurus Lacepede. In a recent revision of the South African ariids, Taylor (1986) reinstated Galeichthys as the valid generic name. Wheeler & Baddokwaya

(1981) demonstrated that Tachysurus was not an ariid catfish since it had a rayed adipose fin, nasal barbels and only one nostril on each side of the head. The genus Arius differs from Galeichthys in having seven anterior fused vertebrae (five in Galeichthys), and an epiotic lamina broadly fused with the transverse process of the 4th fused vertebra (remote from fused vertebral complex and epiotic not forming part of the skull roof in Galeichthys), (Taylor op. cit.). While three species, namely G. ater Castelnau, G. feliceps Valenciennes and G. ocellatus Gilchrist and Thompson were originally described, G. ocellatus was subsequently found to be a junior synonym of G. feliceps.

Prior to this study little was known about the biology of either species. Some information had been published on stomach content analyses and aspects of reproduction in estuarine occurring G. feliceps (Marais & Baird 1980, Coetzee & Pool 1984, Marais 1984, Marais & Venter 1987). However, nothing was known about G. feliceps in the marine environment, and Galeichthys ater had not been studied at all.

This study was originally motivated by the presence of the two species in the catches of the commercial linefishery at Port Alfred. It was evident that, in terms of reproduction, they were vastly different from the other species in the fishery, the majority of which were highly fecund broadcast spawners. The two ariids are mouth-brooders with very low fecundity. A preliminary assessment of the fishery during 1984 demonstrated that while G. feliceps and G. ater represented what was essentially a by-catch, they nevertheless formed a substantial component of the annual catches at Port Alfred (Hecht & Tilney 1989). The question immediately arose as to how they were able to withstand the same rate of exploitation as the more fecund target species in the fishery. Significantly, and notwithstanding their presumed highly K-selected life-history style, they had

continued to persist in catches long after some of the more fecund sparid species had virtually disappeared through over-fishing. As a result of this finding it seemed obvious that further biological and ecological investigation, in conjunction with a study of the dynamics of the two populations, would serve to enhance our understanding as to how highly precocial or K-selected fish species respond to exploitation.

This study represents an investigation into the biology and ecology of G. feliceps and G. ater off the south-east coast of South Africa, in the vicinity of Port Alfred (Fig. 1). Aspects investigated in detail were reproduction, ontogenetic development, growth rate and population age structure, population dynamics and resource partitioning. The last was prompted by the similar overall gross morphology and simultaneous presence in the commercial catches of the two species, which suggested a similar habitat preference. As logistic obstacles precluded *in situ* investigation of their micro-habitat preferences or of the degree of inter-specific competition for essential resources, a feeding study was undertaken to investigate the nature of resource partitioning between them.

The thesis is structured in the following way. Chapter 2 is an investigation into feeding and resource partitioning, Chapter 3 deals with reproduction and Chapter 4 is a study of the early ontogeny and mouth-brooding behaviour of G. feliceps. The age and growth and population dynamics of the two species are explored in Chapters 5 & 6, and the thesis concludes with a general discussion (Chapter 7).

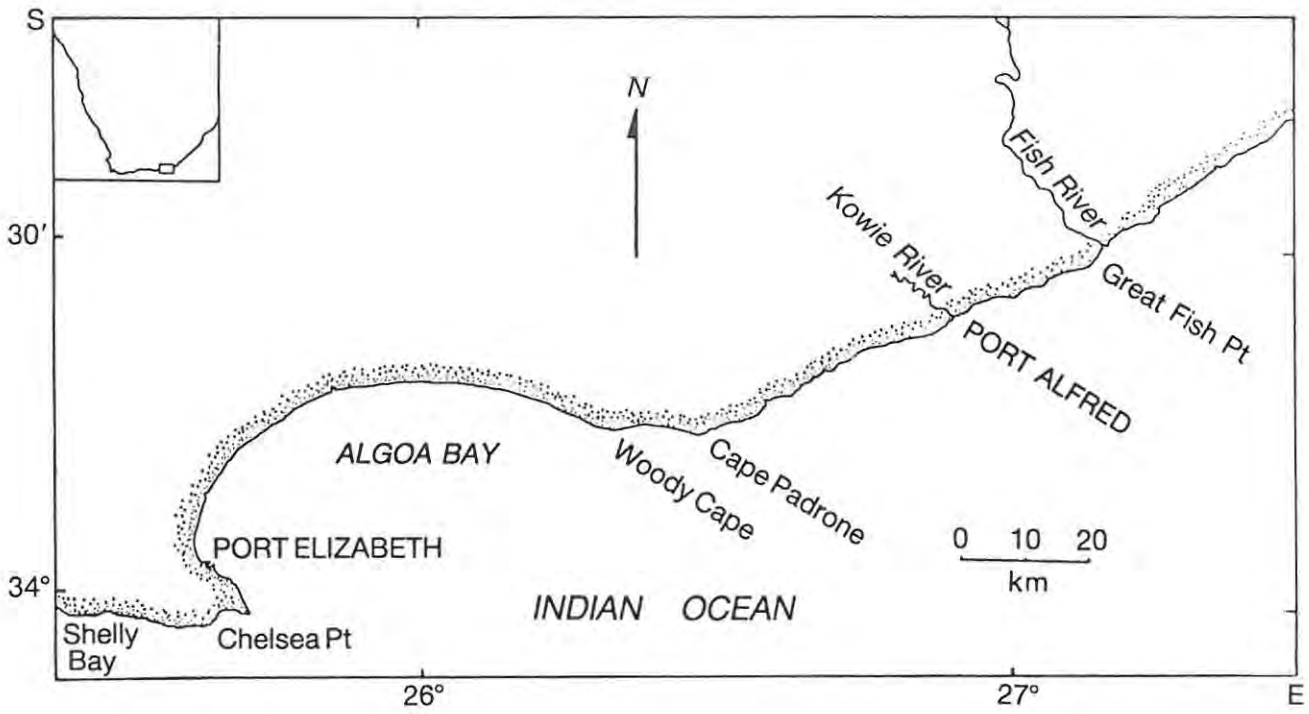


Figure 1: Study area. Sampling was conducted primarily on the commercial fishing quay in Port Alfred on a near-daily basis. The fishery operated between Great Fish Point in the east and Cape Padrone in the west. Estuarine samples were taken from the Kowie River, while some feeding data from the Great Fish and Mtati Rivers were also incorporated. Data from samples collected during a small-mesh trawl survey of Algoa Bay (Buxton et al. 1984) were incorporated, while feeding and growth information for G. ater juveniles were obtained from rotenone samples taken between Shelly Bay and Chelsea Point west of Port Elizabeth (Smale & Buxton 1989).

CHAPTER 2 - FEEDING

Introduction

Resource partitioning is widely accepted as being the prime mechanism allowing the co-existence of species assemblages and communities and it is evident that species commonly partition one of three resources, namely space, food or time of resource utilisation (see review by Schoener 1974). Since Galeichthys feliceps and G. ater could not be observed *in situ*, it was hoped that detailed feeding studies would provide an insight into the degree of interspecific interaction between them in their natural environment. As the two species were highly similar morphologically it was envisaged that they would compete for the available resources and that these would be partitioned between them.

An attempt at integrating functional morphology and ecology was made by investigating the feeding associated morphologies of the two species. Aspects such as dentition, gape size, gill raker morphology, lateral line complexity, olfactory rosette structure and the function of the circum-oral barbels were explored.

The aims of this feeding study were therefore to ascertain the micro-habitats, diets, and feeding strategies of the two species, to investigate whether resource partitioning occurred, and if so, to establish the nature of resource partitioning between them.

The feeding of G. feliceps has previously been studied in the Swartvlei estuarine system (Coetzee & Pool 1984) and the Gamtoos, Krom, Sundays and Swartkops estuaries (Marais 1984). The general feeding habits of G. feliceps have also been described by Day et al. (1981), Smith & Heemstra (1986) and Van der Elst (1981), but prior to this study (Tilney & Hecht 1990)

no published work existed on the feeding habits of G. ater, or of G. feliceps in the marine environment.

Elsewhere in the world, recent ariid feeding studies have been published on Galeichthys caerulescens (Yáñez-Arancibia 1977) in Mexican coastal lagoons, Tachysurus tenuispinis (Mojumder & Dan 1979) in Indian coastal waters, Netuma barba, N. planifrons and Genidens genidens (Araújo 1984) and Netuma barba (Reis 1986a), in Brazilian coastal lagoons, and Arius thalassinus (Euzen 1987) in the Persian Gulf. The studies revealed that all ariids are benthic predators feeding primarily over soft substrata on crustaceans, polychaetes, molluscs, fish and in some instances, detritus.

Materials & Methods

Galeichthys feliceps (FL 232-360mm) and G. ater (FL 195-322mm) were collected from the catches of the Port Alfred commercial ski-boat fishery. The fishing grounds extend from Great Fish Point in the east to Cape Padrone in the west (Fig. 1). Samples were collected on a monthly basis between March 1984 and March 1987. Stomachs of juvenile G. feliceps (FL 46-145mm) from the marine environment were obtained from the collection made on the R.V.Thomas B. Davie during an inshore small mesh trawl survey of the Cape south coast during 1982 (Buxton et al. 1984). Stomach content data for G.ater juveniles (FL 48 - 127mm) were obtained from rotenone collections made in sub-tidal gullies between Schoenmakerskop and Marine Drive, Port Elizabeth (Smale & Buxton, 1989) between September 1984 and September 1985.

To determine the extent of feeding in estuaries by G. feliceps, gill nets were deployed in the Kowie River on a monthly basis between March 1984 and March 1987. Bottom-set gill nets (25, 40, 60, 75, 100 & 150 mm stretched mesh) were used at three localities at approximately 3.5, 4.5 and 5.5 km from the mouth

of the estuary. Gill netting was conducted at neap tides and preliminary trials revealed that the most effective sampling period was between dusk and dawn. Nets were checked and fish removed every two hours in order to prevent predation by the mangrove crab (Scylla serrata), cuttlefish (Sepia officinalis vermiculata), and isopods (Exosphaeroma sp.). Formalin (10%) was injected into the abdominal cavities of fish to halt digestion of stomach contents.

Juvenile G. feliceps (FL 45-55mm) smaller than those caught with gill nets were captured at night in shallow marginal areas of the Kowie river between December and March using a cast net and a search light.

The feeding behaviour of G.feliceps eleuthero-embryos during the buccal incubation phase was investigated by removal of young from mouth-brooding adults, caught in the gill nets.

Feeding data for G. feliceps (FL 47 - 385mm) collected from the Great Fish and Mtati estuaries between April and July 1983 were also incorporated. The material was collected by the late B. E. Trowe of the Department of Ichythyology & Fisheries Science, Rhodes University.

The entire digestive tract was removed and preserved in 10% formalin shortly after sampling. During analysis each stomach and intestine was designated a subjective fullness index between 0 (empty) and 5 (maximum distension), and intestine length was measured between the pyloric sphincter and the vent. By making a longitudinal incision of the stomach to expose the contents, large prey items were removed using forceps, while small food particles and remains were flushed into a petri-dish using water. Stomach contents were examined and sorted into taxa under a binocular microscope. Intact prey items were identified to species level and prey remains to the lowest taxon possible.

Stomach contents were analyzed using four methods:

a.) Numerical occurrence: The number of individuals of each prey type in all stomachs was expressed as a percentage of the total number recorded.

b.) Frequency of occurrence: The number of stomachs in which each prey item occurred was expressed as a percentage of the total number of stomachs in the sample.

c.) Gravimetric method: Prey were blotted and weighed before drying to constant mass at 60 °C to determine the wet : dry weight ratio (Hynes 1950; Hyslop 1980).

d.) Energy contribution: Published energy values for individual taxa (Table 1) were used to convert gravimetric data into energy content in kilojoules per gram (kj/g). The energy contribution of each food type for all stomachs was expressed as a percentage of the total energy (Whitfield 1980). Since the frequency with which a particular prey organism occurs in the diet is a measure of a degree of dependence by the predator on that organism, the product of the percentage frequency of occurrence (%FO) and percentage energy (%E) values was expressed as an index, termed the Energy Index (EI), as follows:

$$EI = \%FO \times \%E$$

Vacuity indices based on the percentage ratio of empty stomachs to the total number of stomachs in the sample were calculated. A low vacuity index is an indication of a voracious predator (Euzen 1987).

Feeding seasonality was investigated in the marine samples. Data for each quarter were grouped according to season and sex. The seasonal trend of stomach fullness was similarly determined using the stomach fullness indices.

Statistical methods were used in an attempt to quantify diet overlap between the two species in the marine environment. Measurements of niche or resource overlaps have been

demonstrated by several authors using different techniques, namely overlap indices in combination with Cochran's chi-squared test (Schoener 1970), the overlap measure of Morisita (1959 as modified by Horn 1966 in Zaret & Rand 1971) and Spearman rank correlation coefficients in conjunction with t-tests (Fritz 1974).

Table I. Wet:dry weight ratios and energy values of food taxa used in the construction of Energy Indices.

Taxa	Dry wt. (%)	Energy (Kj/g)	References
Crustacea			
Amphipoda	26	14.47	Whitfield (1980)
Anomura			
Calianassa kraussi	21	21.24	Whitfield (1980)
Upogebia africana	30	14.49	Hanekom (1980)
Brachyura	25	13.30	Whitfield (1980)
Isopoda	28	14.62	Whitfield (1980)
Larvae	33	17.94	Blaber (1979)
Macrura	17	20.30	Whitfield (1980)
			Cockroft & McLachlan (1987)
Mysidacea	11	19.44	Cockroft & McLachlan (1987)
Echiurida			
Ochaetostoma capense	18	21.70	This study
Mollusca			
Cephalopoda	22	22.58	Buchan & Smale (1981)
Pelecypoda - flesh	7	20.28	Berry (1978)
Mucus	5	15.05	Gorlick (1980)
Polychaeta	28	18.57	Whitfield (1980)
Teleostei	18	24.40	Whitfield (1980)
Scales	31	8.52	Whitfield & Blaber (1978)

Since stomach content analyses revealed that 61% of G. feliceps juveniles between 54-225 mm (FL) had scales in their stomachs to the exclusion of any other teleost remains, two experiments were conducted in order to ascertain whether G. feliceps juveniles are lepidophagous or whether the scales were

scavenged. Experimental procedure was adapted from Whitfield & Blaber (1978).

Experiment 1. Four G. feliceps juveniles (FL 65-85mm) were starved for 48 hours and put into an aerated 50 litre glass aquarium. Scales (n=125) removed from living Liza richardsonii, Rhabdosargus holubi and Pomadasys commersonni were introduced. After one hour the remaining scales were counted.

Experiment 2. Three individuals from each of the above mentioned species (FL 80-150mm) were placed into a second tank together with four similarly starved G. feliceps juveniles. After 120 hours the G. feliceps digestive tracts were examined for the presence or absence of scales.

In an attempt to assess the relative importance of sight, smell and taste in the location of food, a series of preliminary aquarium observations were conducted using G. feliceps juveniles. Individuals which had been deprived of either their sight, smell or taste were placed into separate, 100 litre aquaria. An untreated animal held in a fourth aquarium was used as a control. Food-finding efficiency was measured by recording the time taken to locate and ingest a $3mm^2$ particle of food introduced into the water at a point distant from the animal. A 15 minute interval between successive tests was used to ensure that the fish were not engaged in appetitive searching behaviour prior to food introduction.

Morphological adaptations for feeding were investigated as follows: The dentition and circum-oral barbels of G. feliceps and G. ater were examined using scanning electron microscopy. Procedures according to Cross (1985) for the preparation and processing of material for electron microscopy were followed. Gill raker size and spacing were measured using vernier calipers while the structure of the olfactory rosettes and the extent of the lateral line were determined using a binocular

microscope. Stomach pH of freshly sacrificed and dissected animals was measured using Merck pH indicator strips (pH 0-14).

Results

Anatomical adaptations for feeding

Galeichthys species are equipped with three pairs of circum-oral barbels, one maxillary and two dentary. They are capable of a certain degree of movement and can be held erect or laid flat against the body. In the erect position, the four mandibular barbels are held at 90° to the body. The longer outer pair are projected laterally at an angle of approximately 25°, so that when searching for food, the tips of all four mandibular barbels are trailed across the substratum. The long maxillary barbels are extended slightly anteriorly and at an angle of approximately 45° from the vertical (Fig. 2a & b). The tips of the maxillary barbels do not touch the substratum during foraging activity and presumably serve to detect prey that has moved off the bottom.

Taste buds constitute a large proportion of the surface area of the barbels of both species (Griffiths 1984; Andrew 1987), (Plate Ia & b), and were found to be most abundant distally, on the leading edges of the barbels. The density of taste buds differed between the two species. Galeichthys feliceps barbels held approximately 90/mm² and G. ater 40/mm² (Andrew 1987). The structure of the taste buds was identical in the two species and was similar to those found on other benthic feeding fishes, e.g. flatfishes (Livingston 1987). The taste buds were raised, oval structures covered with short microvilli around the periphery and longer microvilli toward the centre (Plate Ic & d).

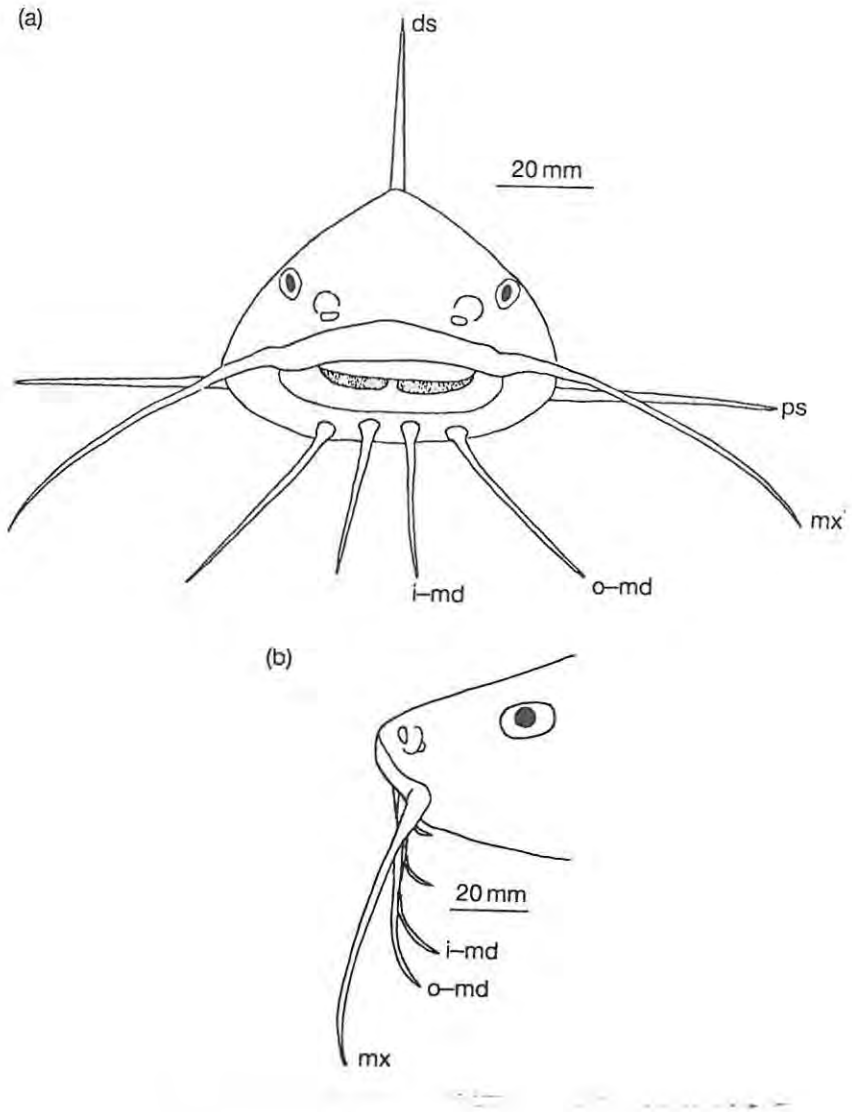


Figure 2. (a) Head-on and (b) lateral view of Galeichthys demonstrating the positions of the maxillary (mx), inner (i-md) and outer (o-md) mandibular barbels during foraging. ds=Dorsal spine; ps=pectoral spine.

The mouth is slightly subterminal, of intermediate size, and has fleshy lips. During prey ingestion the body is orientated at approximately 35° from the horizontal, the angle required to bring the mouth into contact with the substratum. Aquarium observations of feeding animals demonstrated that prey was often detected using the mandibular barbels which were trailed over the substratum behind the mouth. When this occurred, the animal came to an immediate halt by abducting the pectoral fins, which also acted as a pivot about which the body tilted in order to assume the feeding posture described above.

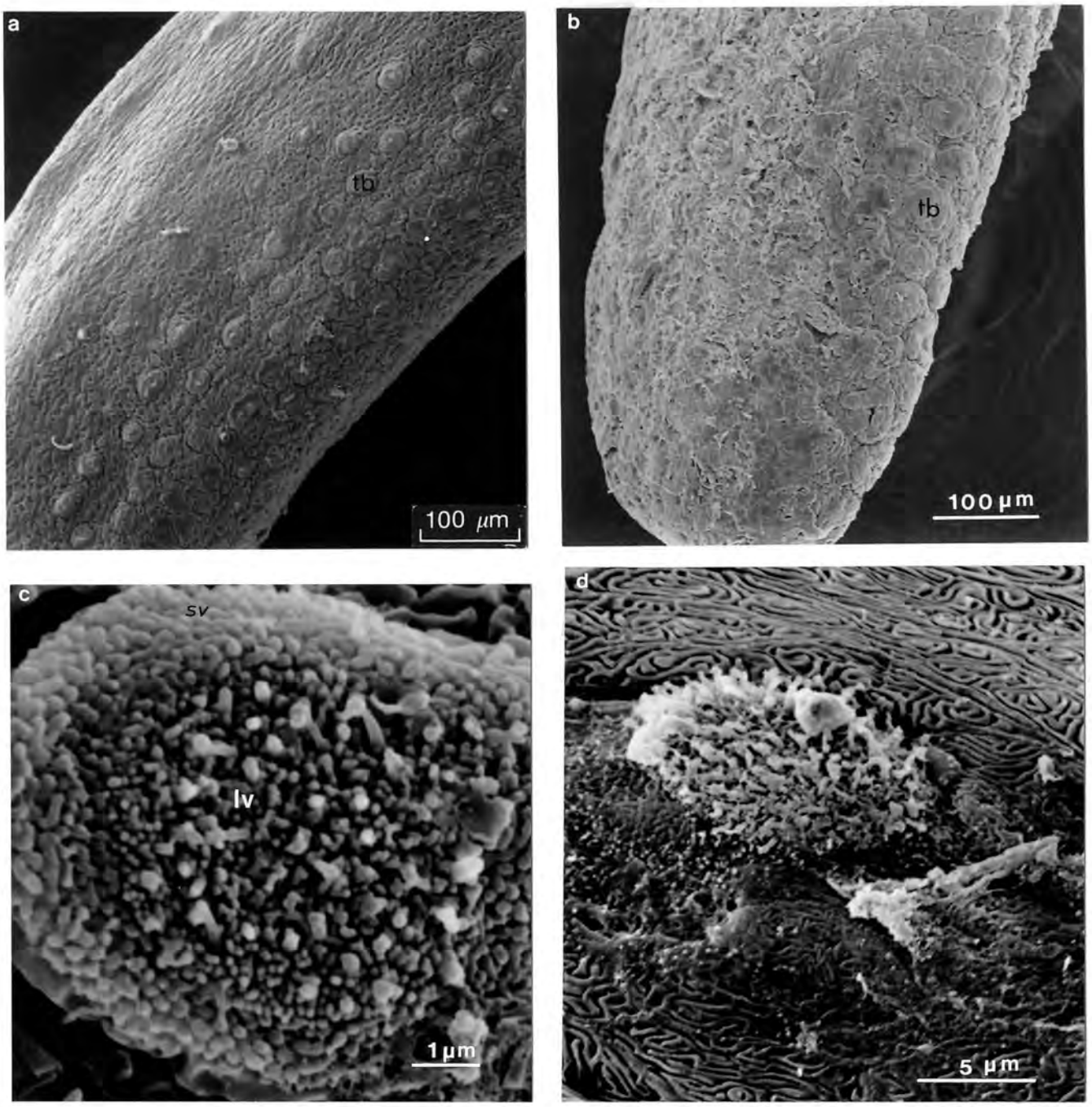


Plate I. (a) Taste bud (tb) distribution on circum-oral barbels of G. feliceps and (b) G. ater. (c) Taste bud structure in G. feliceps and (d) G. ater illustrating their similarity. sv=Short villi; lv=long villi.

While the tail moved upwards and slightly anteriorly, the head moved downwards and slightly posteriorly, resulting in the mouth being positioned directly over the detected prey item.

Ingestion of benthic prey occurred while the animal was stationary. The suck and grasp method of prey capture common to many modern siluroids (Gosline 1973) was employed, in which a lowering of the hyoid complex sets up a negative pressure in the vicinity of the prey when the mouth is opened (Alexander 1970; Lauder & Clarke 1984; Osse et al. 1985 and Van Leeuwen & Miller 1985). This results in a net inflow of water into the buccopharyngeal cavity, carrying the prey with it into the mouth.

The oesophagus is short and distensible, leading to a muscular J-shaped stomach. The stomach environment is acidic, the pH ranging between 2.0 and 6.0 in feeding G. feliceps. Feeding ceases during mouth brooding (see Chapter 4), and stomach pH varies between 8.0 and 9.0 in these individuals. The anteriorly directed pyloric sphincter leads into a thin-walled intestine. The mean ratio of body length (FL) to intestine length for all size classes is 1:1.78 (±0.24) for G. feliceps and 1:1.79 (±0.21) for G.ater.

Since very little processing of prey occurs within the buccal cavity, the teeth are small and serve to grasp prey before it is swallowed whole. The tooth structure was similar for the two species (Plate IIa & b). Several rows of small, recurved, villiform teeth occur on the dentary, pre-maxilla, palate and on two pharyngeal plates on the roof of the mouth.

The gill rakers, which are short and stout (mean length 2.97mm ±1.37mm), occur on both anterior and posterior margins of the gill arches and on the pharyngeal surface opposite the posterior margin of the fourth gill arch. Excurrent water expelled between the first gill arch and the operculum is strained through proportionately longer gill rakers found on the anterior margin of this gill arch. Gill rakers of adjacent gill arches are interdigitating, resulting in an effective, but inefficient, low sieve-potential filtering mechanism (Lagler et al. 1977).

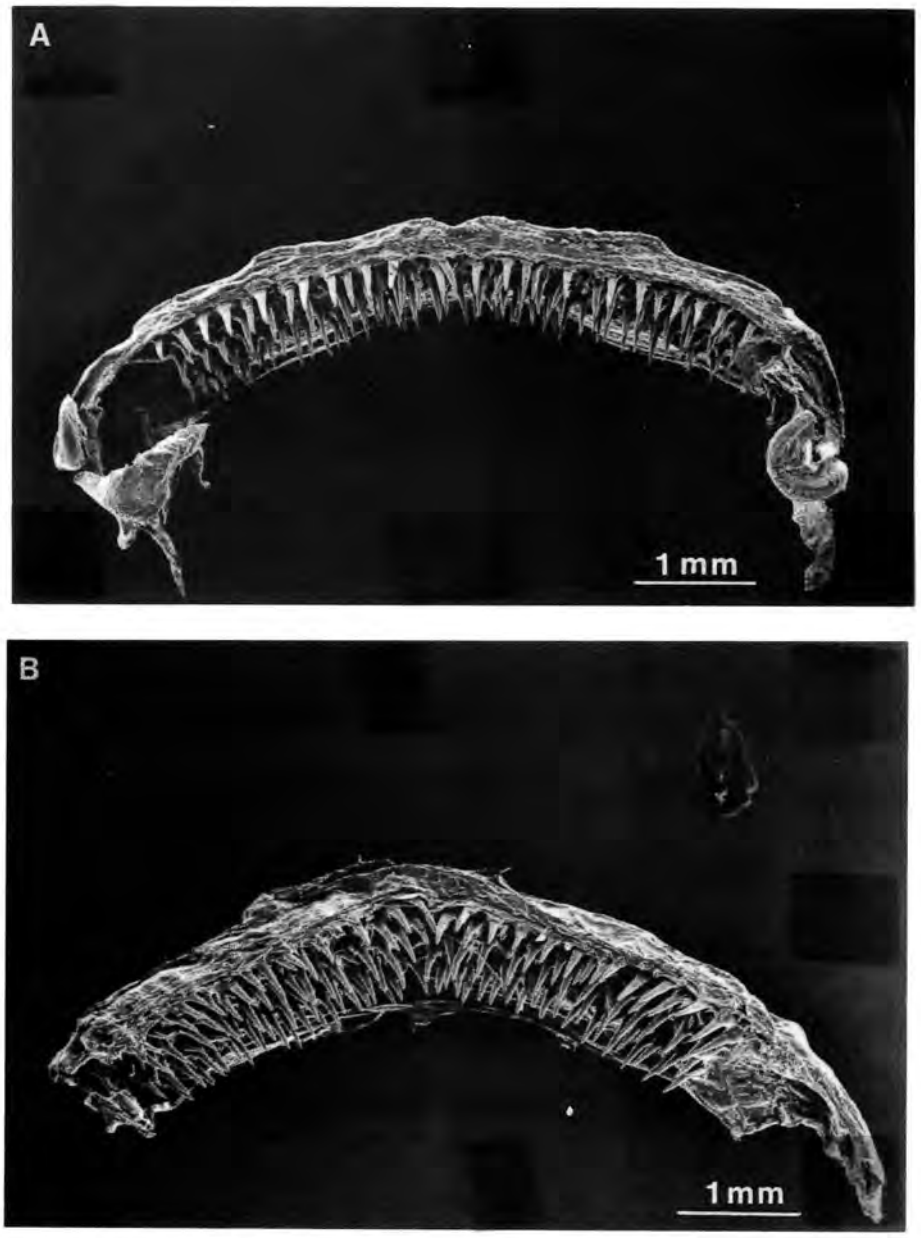


Plate II. Scanning electron micrograph of the maxillary teeth of (a) G. feliceps and (b) G. ater juvenile showing the similarity in structure.

It is likely that they serve primarily to protect the delicate respiratory lamellae against abrasion and damage by the ingested, live food. The mean gap size between opposing, interdigitating gill rakers is 0.23mm (±0.22mm) in adult G. feliceps, enabling the filtration of larger zooplankton (e.g. mysids and macruran shrimps).

The oval nasal chambers are divided into two nares by a dividing bridge of skin, which when flattened completely covers the posterior naris and restricts water flow into the olfactory chamber. The septum is supported by a cartilaginous rod and may be raised to form a ridge that directs water into the anterior naris, through the nasal chamber and out via the posterior naris. The numbers of sensory lamellae forming the olfactory rosettes ranges between 10 in juveniles and 60 in adults of both species and are accompanied by a change in shape of the olfactory rosettes from ovoid to elongate.

The laterally positioned eyes are of moderate size, ranging between 4.9% (±0.12%) and 3.4% (±0.1%) of total body length in juvenile and adult G. feliceps respectively. In G. ater the eyes are 4.4% (±0.23%) of total body length in juveniles and 3.7% (±0.24%) in adults. They are capable of lateral and vertical movement within their sockets, affording a wide field of periscopical and a certain degree of binocular vision. Galeichthys are relatively photophobic and their vision in daylight appears to be poor, as suggested by their inability to detect live prey from a distance of more than a few centimeters (pers. obs.). While their sight is probably more effective at lower light intensities, the extent to which it is used in prey capture is unknown.

The lateral line between the caudal peduncle and the pectoral girdle gives rise to regularly spaced, oblique dorsal and ventral branches, of which the latter are longer and may be branched. In the region anterior to the pectoral girdle the lateral line branches extensively, dorsally over the nape area, ventrally over the cleithral region and anteriorly onto the head. The dense network on the head extends over the opercular, infra-orbital and cranial areas extending anteriorly to the upper lip. The lateral line system increases in extent with growth, reaching maximum complexity at approximately the size of sexual maturity (Fig. 3). It is not known whether Ampullae of Lorenzini are present in the lateral line system, although

they are thought to occur in clariids (Lissman & Machin 1963) and plotosids (Bullock 1973).

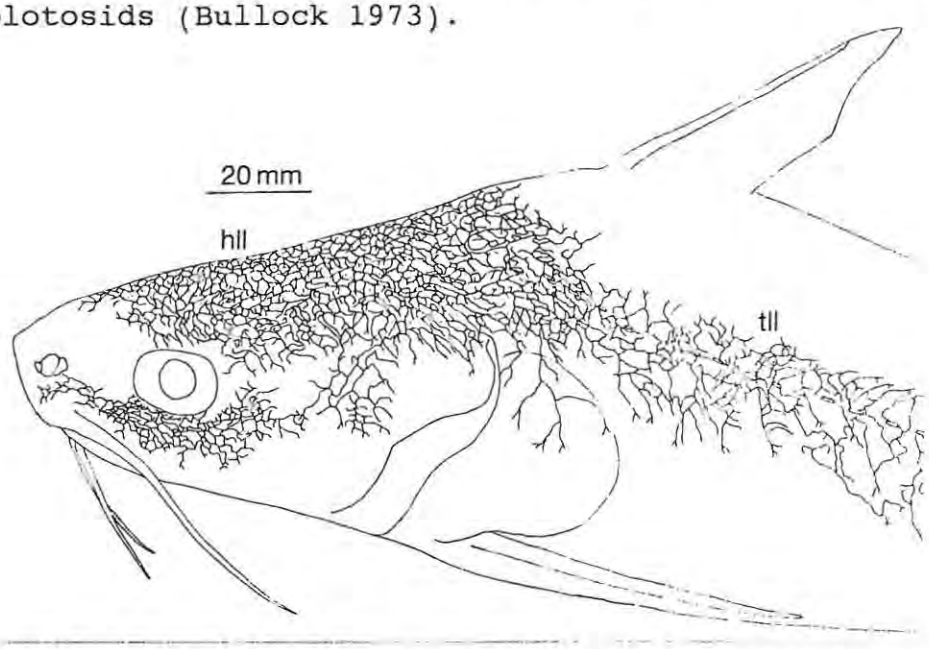


Figure 3. Diagrammatic reconstruction of the lateral line system of Galeichthys. hll=Head lateral line; tll=trunk lateral line.

The caudal fin structure differed in the two species and may be a reflection of different mobility (speed) requirements during foraging. In G. feliceps the caudal fin is deeply forked with the upper lobe being longer than the lower, while G. ater has a feebly forked caudal, verging on emarginate (Fig. 4).

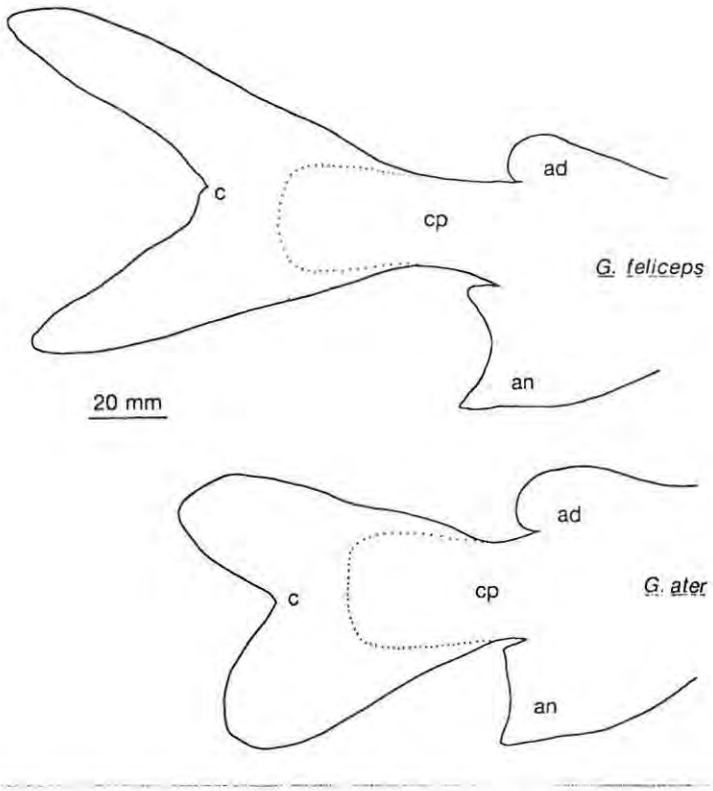


Figure 4. A comparison of the caudal fin structure between similar sized G. feliceps and G. ater. ad=Adipose fin; an=anal fin; c=caudal fin; cp=caudal peduncle.

Diet: Offshore samples

The principle taxa in the diet of G. feliceps were brachyura (49% of total energy in the diet), echiurida (27%) and polychaeta (17%), (Fig. 5a). Two species of crab namely Thaumastoplax spiralis and Goneplax angulata made up the bulk of the crustacean component. A single species of echiurid, Ochaetostoma capense occurred in the diet. Day (1974) remarked that T. spiralis and O. capense have a commensal relationship and share a common burrow, explaining the co-occurrence of these two animals in G. feliceps stomachs. The most commonly consumed polychaete was the sedentary Sternaspsis scutata (Appendix Ia).

Galeichthys feliceps prey exclusively on soft substratum dwellers. The crabs G. angulata and T. spiralis are sand burrowers (Barnard 1950; Day 1974), O. capense and S. scutata

burrow in mud (Day 1967, 1974) and the bivalve Phaxas decipiens burrows in sandy and muddy substrata (Kilburn & Rippey 1982). The most important taxa in the diet of G. ater were brachyurans, isopods, polychaets and cephalopods (Fig. 5b). The Cape rock crab Plagusia chabrus and it's megalopae were the most common brachyuran in the diet, while Dehaanius dentatus and Macropodia falcifera were frequently encountered. The anomuran Galathea dispersa and the palinuran Scyllarides elizabethae (juveniles) were also important. A number of large chelae, probably the result of tackling crabs too large to ingest, also occurred. The polychaetes were generally difficult to identify as a consequence of their rapid digestion in the stomach. Most, however, belonged to the group errantia, and included Eunice spp., Lysidice natalense and Platynereis dumerilii. The sedentary Pherussa sp. was also well represented. Juvenile Octopus vulgaris were the most abundant mollusc in the diet, while the Cymodose spp. isopods, especially C. valida, and caridean shrimps were other important prey items (Appendix Ib).

In contrast to G. feliceps, the prey of G. ater consisted of both reef- and soft substratum-dwelling species. Plagusia chabrus (5.5% of dietary energy) and D. dentatus (2.8%) are reef dwellers, while O. capense (5%) occurs in mud. G. dispersa (2.9%), the palinuran S. elisabethae (1.5%) and the various isopods (10.3%), polychaetes (12.8%) and cephalopods (12.8%) occur over both hard and soft substrata (Day et al. 1970; C. Buxton, Dept. Ichthyology & Fisheries Science, Rhodes University, pers. comm.).

Prey common to both species included O. capense, four crabs G. angulata, H. orbiculare, Philyra punctata and Atelecyclus septemdentatus, an isopod Synidotea hirtipes, the cephalopod O. vulgaris and a polychaete Pherussa sp.. While there were only eight common species in their diets, they shared 13 out of a total of 20 food taxa.

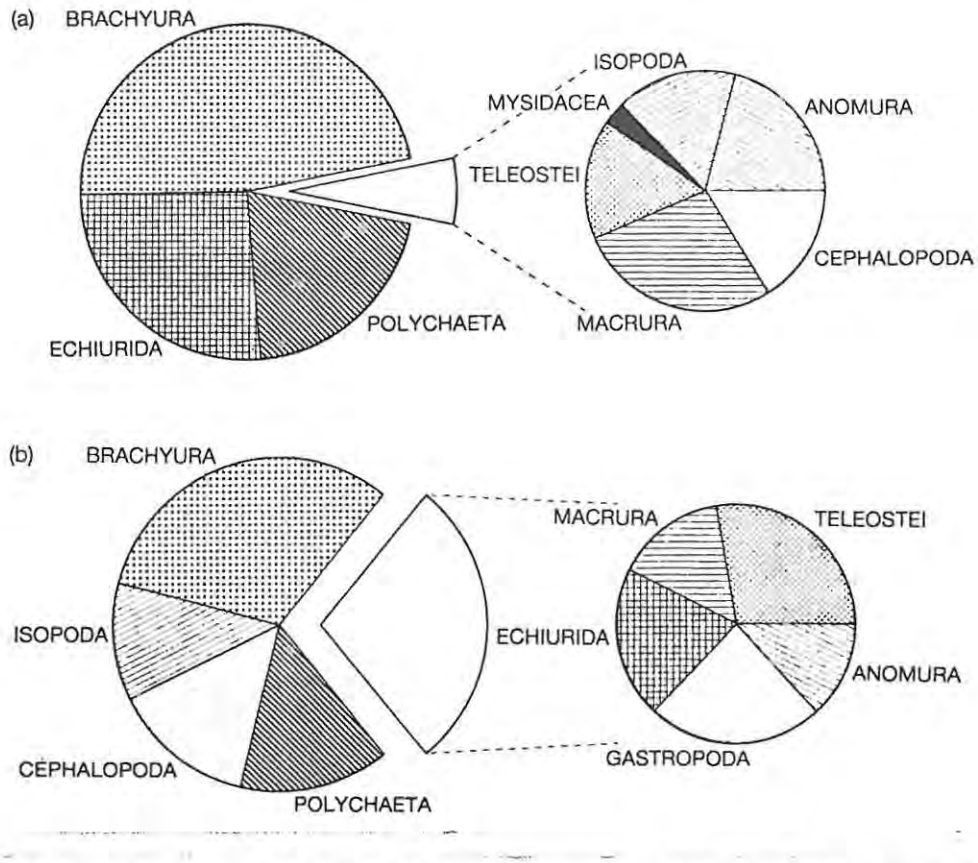


Figure 5. Diets in the marine environment of (a) G. feliceps adults. Wedges represent percentage energy contribution of prey. FL=232-380mm, n=402. (b) G. ater adults. FL=185-322mm, n=285.

The diet of G. feliceps was narrow, with 80% comprising four species, namely T. spiralis (23.3%), G. angulata (19.7%), O. capense (27%) and the sedentary polychaete S. scutata (9.3%). G. ater on the other hand fed more broadly, the largest contribution by a single species being that of P. chabrus (5.5%). The relative numbers of prey species taken by the two species are presented in Table II.

Table II. A comparison of the number of species in the diet of G. feliceps and G. ater sampled in the marine environment.

Taxon	G. feliceps No. of species	G. ater No. of species	Common No. of species
Brachyura	8	15	4
Echiurida	1	1	1
Isopoda	2	22	1
Mollusca	3	5	1
Polychaeta	6	6	1
Total	20	49	8

The data obtained from the R. V. Thomas B. Davie inshore trawl survey showed that G. feliceps juveniles in this environment fed primarily on O. capense (Fig. 6a). Thaumastoplax spiralis, cephalopods, anomurans, mysids, teleost scales, polychaetes and amphipods made up the rest of the diet. Copious amounts of mucus were also present in many stomachs (Appendix Ic). The origin of this material is unclear, although the possibility exists that juveniles may remove mucus from the surface of other fish.

Sub-tidal gully samples

G. ater juveniles inhabiting sub-tidal reefs fed largely on amphipods, isopods and polychaetes (Fig. 6b). The large majority of amphipods were from the sub-order gammaridea, while two isopods, namely Munna sheltoni and Parisocladus perforatus were important. Most of the polychaetes in the diet were from the group errantia. As with G. feliceps, substantial amounts of mucus were found in the stomachs of G. ater juveniles (Appendix Id).

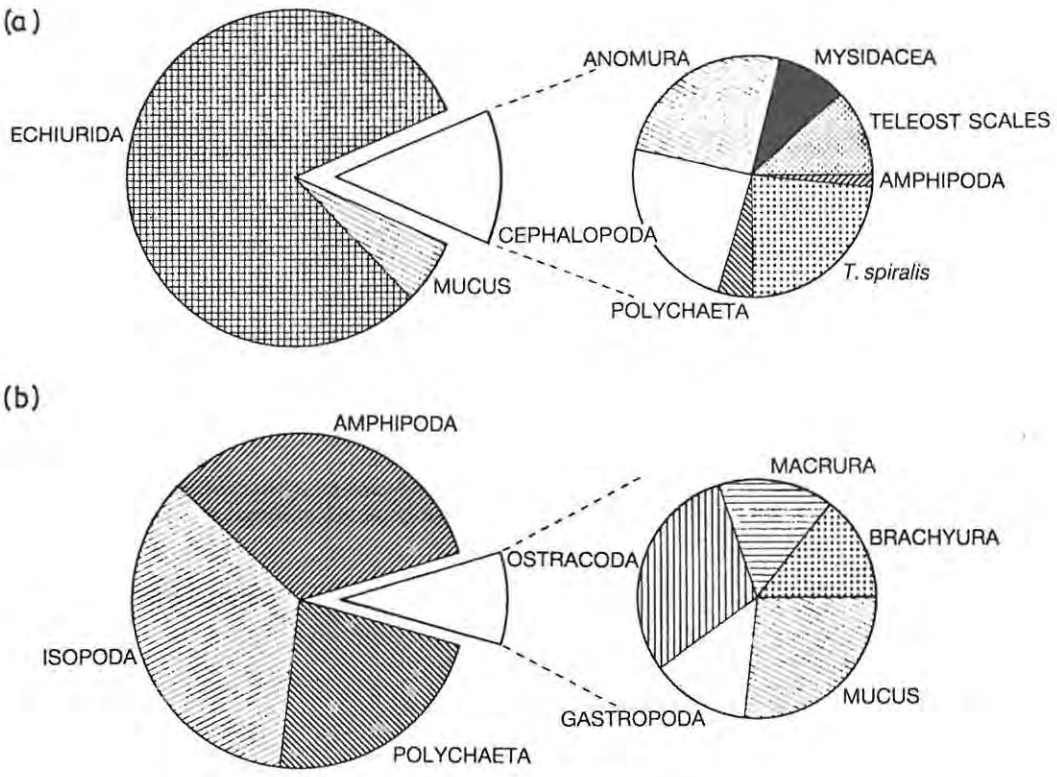


Figure 6. Diets in the marine environment of (a) G. feliceps juveniles. FL=47-175mm, n=48. (b) G. ater juveniles. FL=81-121mm, n=41.

Estuarine samples

While hook and line surveys revealed that adult G. feliceps of both sexes frequent estuaries within 1-2 km of the mouth throughout the year, the gill net survey conducted in the Kowie estuary between 2.5-5.5 km upstream revealed that sexually mature G. feliceps do not forage upriver. A large component of the gill net sample did however consist of mouth-brooding males, which utilise this environment as a refuge between September and March. Stomachs from all mouth-brooding fishes (n=250) were empty, containing only traces of greenish bile-stained mucus. In addition, the diameter of their digestive tracts was considerably reduced, indicating a

complete cessation of feeding activity during the oral incubation phase (see also Chapter 4).

In contrast to adults, juvenile G. feliceps were found to forage in estuaries throughout the year. The most important component in the diet of juvenile G. feliceps in the Kowie estuary was the burrowing mudprawn U. africana (Fig. 7). Three species of crab, C. edwardsii, H. orbiculare and T. spiralis made up the brachyuran component, Exosphaeroma hylocoetes and E. truncatitelson the isopod component, while the teleosts were represented by Atherina breviceps and unidentified remains (Appendix Ie).

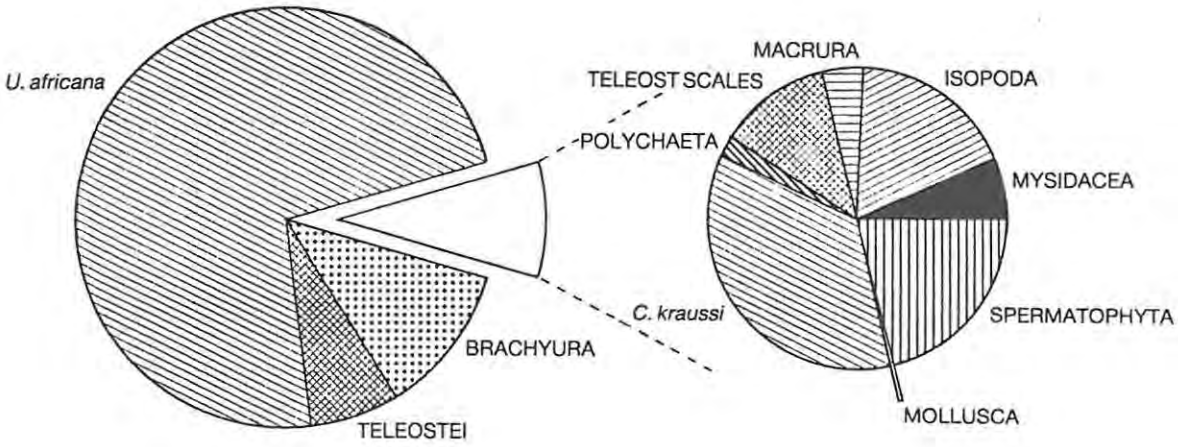


Figure 7. Diet of G. feliceps juveniles in the Kowie River estuary. FL=125-215mm, n=112.

In the Great Fish River estuary, data accumulated over a four month period between April and July 1983 revealed that both juvenile and adult G. feliceps foraged in this estuary within 1-2 km from the river mouth. Sand prawn, crabs, amphipods and teleost scales were important in the diet of juveniles (Fig. 8a). Other taxa in their diet were mysids, polychaetes, macruran shrimps and prawns, isopods and the mud prawn U.

africana. The crabs in the diet included C. edwardsii and H. orbiculare (Appendix If). The adults consumed mainly C. kraussi and teleosts (Fig. 8b). The mud prawn U. africana, crabs, penaeid prawns and mysid shrimps were also present (Appendix Ig).

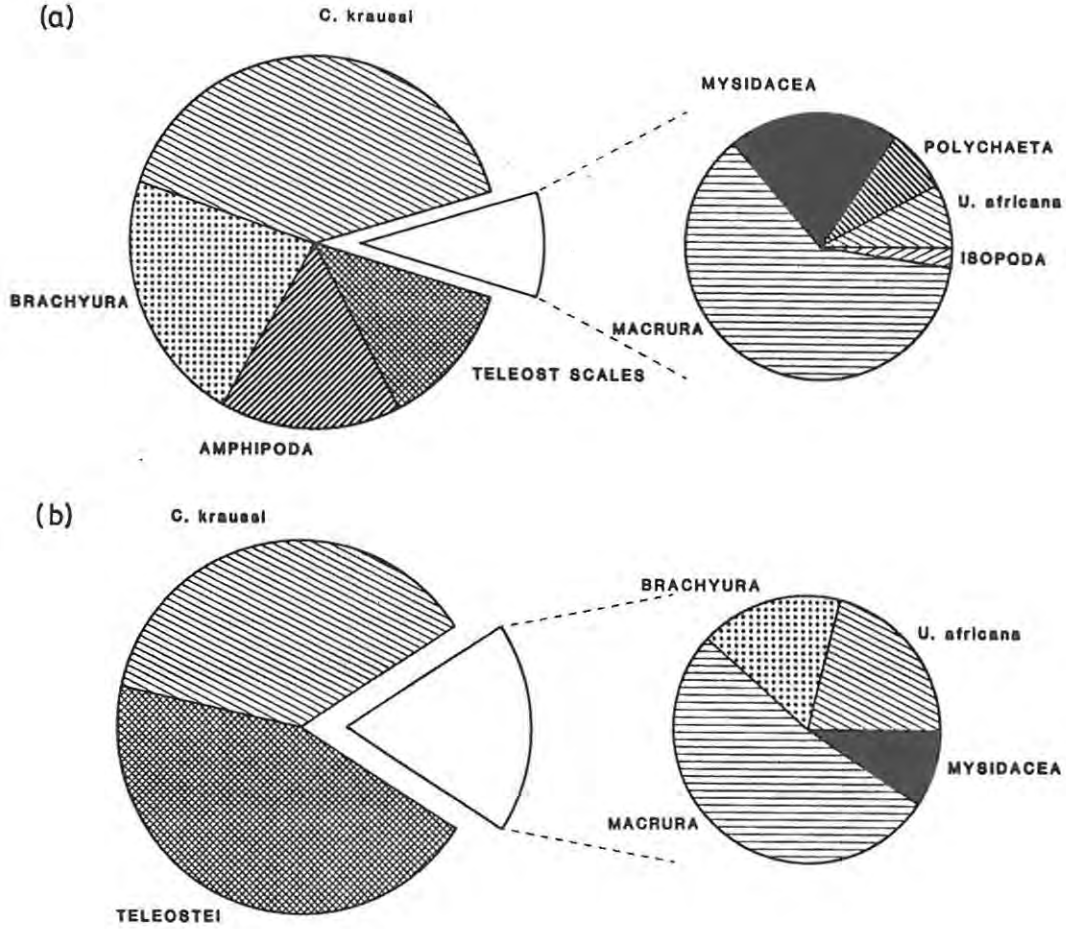


Figure 8. Diets of G. feliceps in the Fish River estuary. (a) Juveniles FL=45-180mm, n=46. (b) Adults FL=255-385mm, n=23.

Only juvenile G. feliceps were encountered in the Mtati River estuary which is closed off from the sea, opening for a brief period (2-3 weeks) during spring each year. They fed mainly on isopods, teleosts and teleost scales (Fig. 9). Sand prawn, C.

kraussi, crabs, amphipods and Zostera sp. also occurred (Appendix Ig). Sample sizes for the Fish and Mtati Rivers were small, but yielded results consistent with those from the Kowie River and the literature (Coetzee & Pool 1984; Marais 1984).

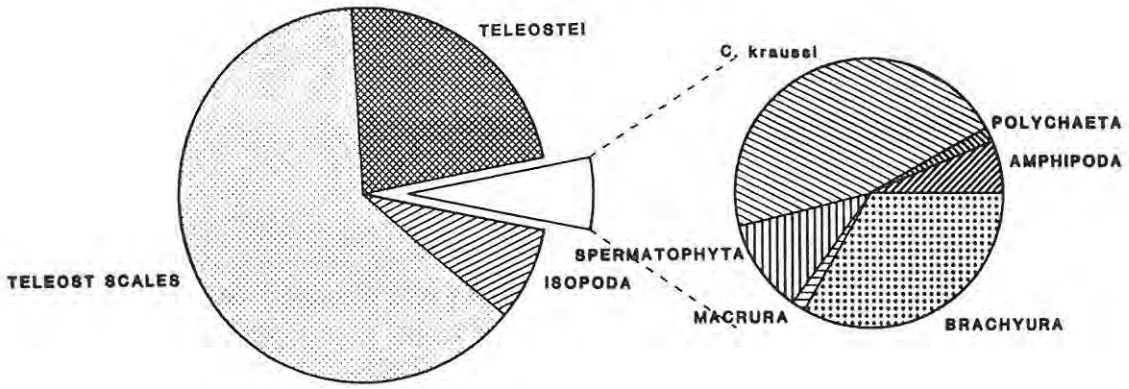


Figure 9. Diet of G. feliceps in the Mtati River estuary. FL=175-214mm, n=38.

Eleuthero-embryo sample

The stomachs of eleuthero-embryos contained mucus and detritivorous material. The latter comprised spermatophyte remains, crustacean exoskeleta, poriferan spicules, mucus and sand (Appendix Ih). Gravimetric data was used to express the diet graphically (Fig. 10). Galeichthys feliceps do not release their young to feed during the incubation phase (see Chapter 4), as is the case in some mouth brooding cichlids (Fryer & Iles 1972). Instead, the adult picks up detritus from the substratum and the young feed within the buccal cavity. This behaviour was confirmed during aquarium observations. The presence of yolk and teleost remains in eleuthero-embryo

stomachs indicate that a degree of sibling cannibalism may occur within the adult buccal cavity. The eleuthero-embryos may also feed on adult buccal mucous during the mouth-brooding phase.

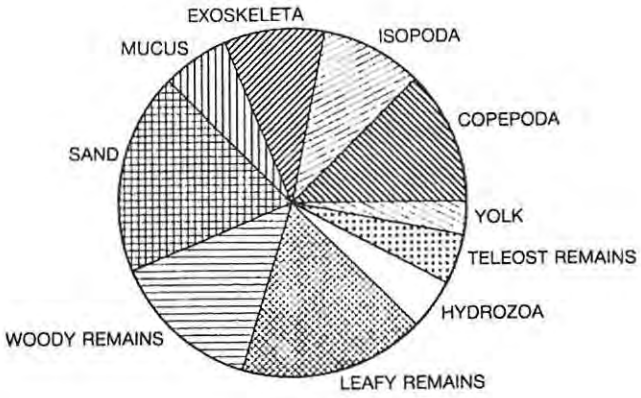


Figure 10. Diet of G. feliceps free-embryos during the mouth-brooding phase. FL=38-45mm, n=57.

Feeding seasonality

The seasonal contribution of important prey in the diets of G. feliceps and G. ater are presented in Figure 11, and the seasonal variation in mean stomach fullness is plotted in Figure 12.

The seasonal variation in food composition was similar for both sexes in G. feliceps. Brachyura were important all year round, being most well represented in summer and spring. Polychaetes were abundant in autumn and echiurids in winter. Molluscs were a relatively minor component in their diet but were well represented in summer. In G. ater, brachyura, isopoda and polychaeta were important throughout the year, with polychaetes being particularly well represented in spring. Cephalopods, teleosts and macrura were less important in the diet, with no seasonal pattern.

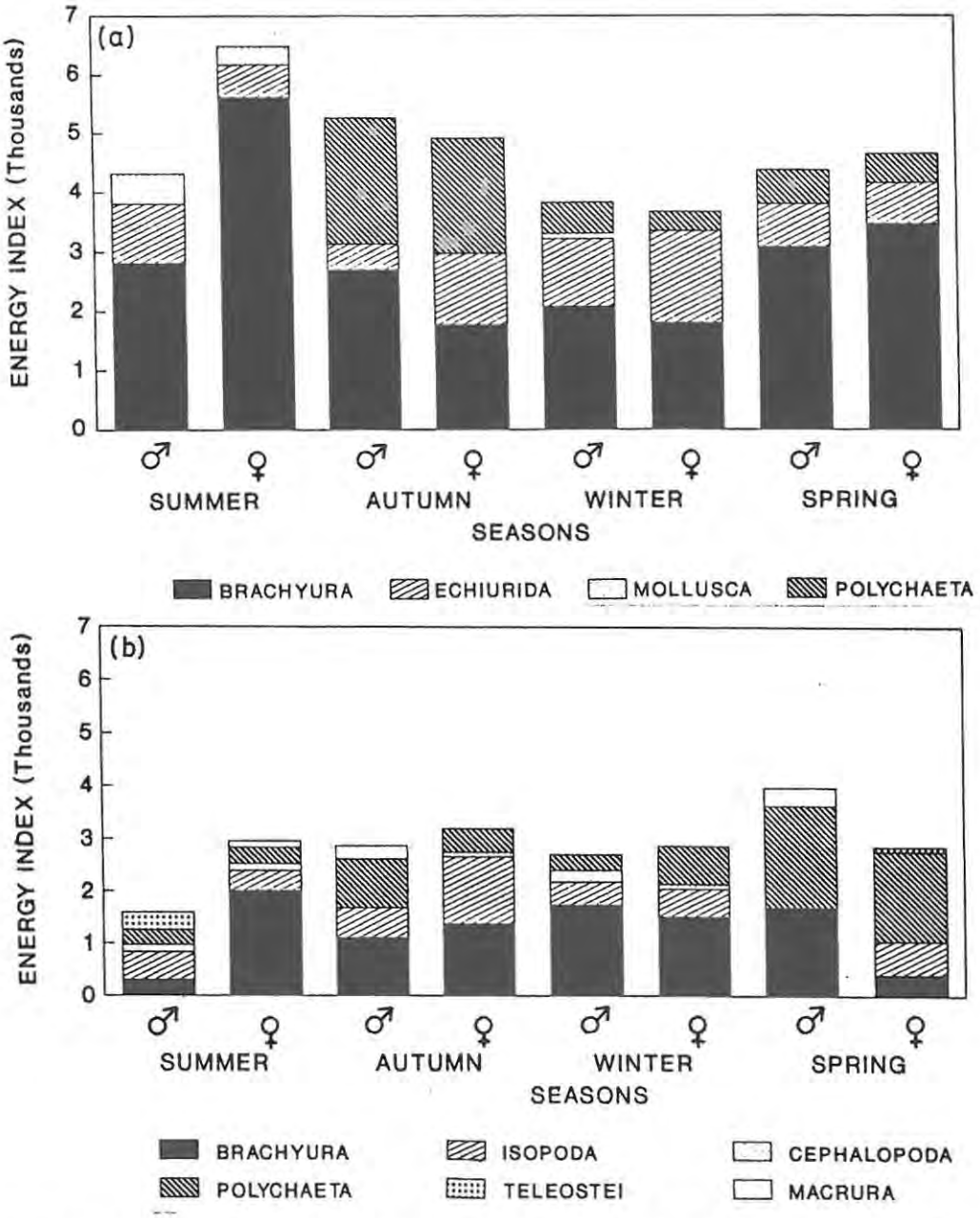


Figure 11. Feeding seasonality in (a) G. feliceps and (b) G. ater males and females in the marine environment.

There was little seasonal variation in mean stomach fullness in G. feliceps. The fullness indices were slightly higher in summer and autumn, while males had fuller stomachs in summer and winter than did females. The maximum stomach fullness recorded, expressed gravimetrically as a percentage of total body mass, was 4.05%. The maximum stomach fullness value recorded for G. ater was 4.01%. The mean stomach fullness indices remained constant throughout the year. Male stomachs

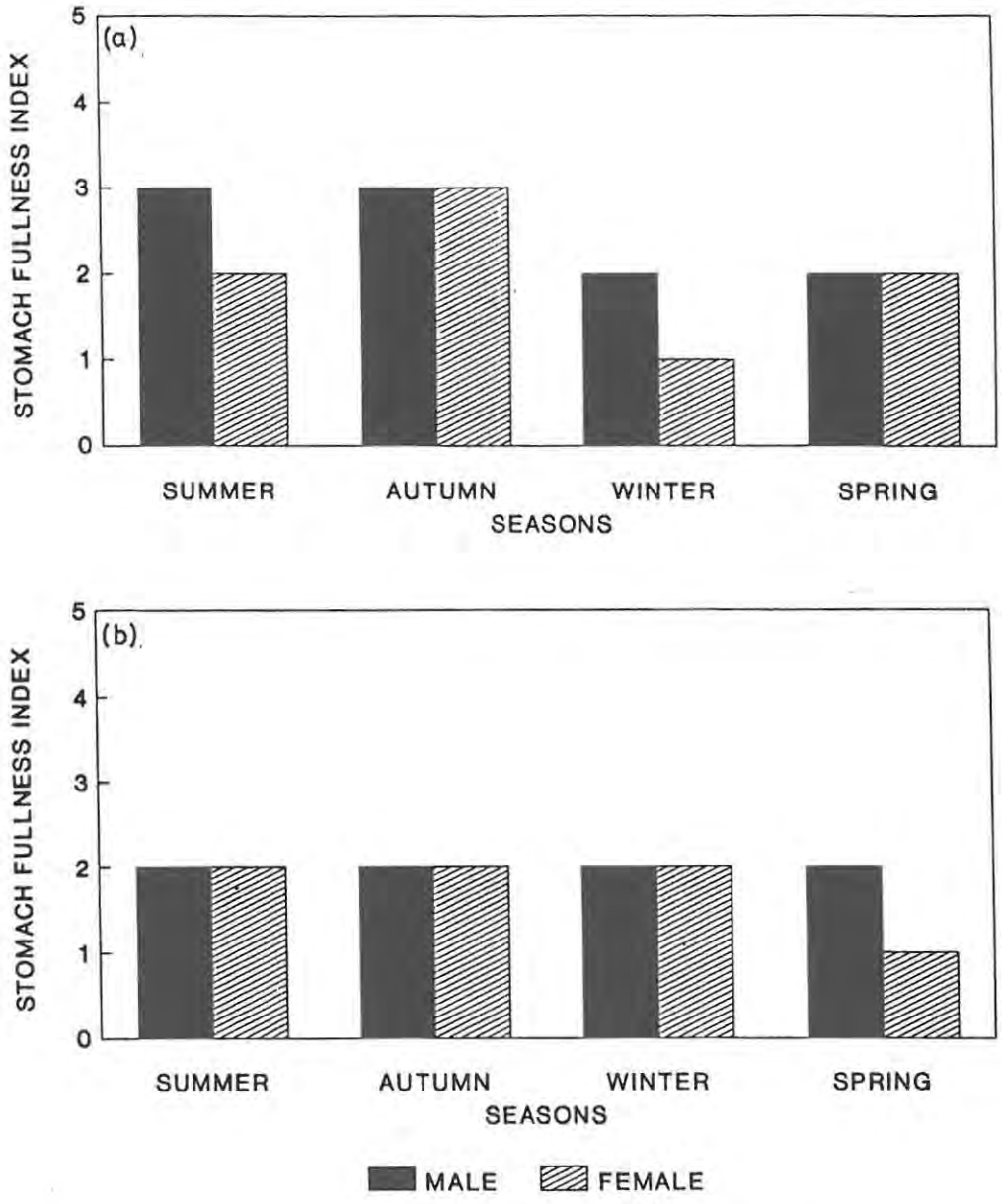


Figure 12. Seasonal stomach fullness indices of (a) G. feliceps and (b) G. ater males and females in the marine environment.

were fuller than female stomachs in spring. While G. feliceps stomachs were generally fuller than those of G. ater throughout the year, the stomach vacuity indices of 14% and 11% for the two species respectively indicate that they fed at similar intensities. Comparisons of stomachs with food vs.

empty stomachs for the two species in the marine environment revealed significant seasonal differences for G. feliceps (X^2 = 20.94, df = 3, P < .01), in which stomachs with food occurred most frequently in summer (95.5%), followed by spring (92.6%), autumn (86.2%) and winter (73.1%). There were no significant seasonal differences at the 5% level for G. ater (X^2 = 2.66), in which stomachs with food occurred as follows: Summer (90.5%), spring (86.2%), autumn (82.1%) and winter (90.6%).

In the marine environment there was a marked shift in dietary preference with growth between juveniles and adults. The bulk of the juvenile G. feliceps diet consisted primarily of echiurid worms (Fig. 6a), while in adults, crabs, polychaetes and echiurids were all major food items (Fig. 5a). Amphipods were an important dietary component in G. ater juveniles (Fig. 6b). In adults they were absent, being replaced by crabs and cephalopods (Fig. 5b). In estuaries the diets of juveniles and adults were similar (Figs. 7, 8 & 9), although the sample of adults in this environment was small.

The lepidophagy question

Experiment 1. The G. feliceps juveniles responded immediately to the introduced scales by engaging in appetitive searching. After one hour the experimental animals had reached satiation and 89% of the scales had been consumed.

Experiment 2. All four G. feliceps digestive tracts were empty after 120 hours. Visual observations indicated that their behaviour appeared to be unaffected by the introduced fish.

The importance of sight, smell and taste in food location

a) The untreated control animals responded to introduced food after a few seconds by going into an arousal phase (Kleerekoper 1982) of rapid undirected locomotion until the food was located.

b) In the absence of olfactory perception, animals failed to be aroused into a searching mode unless the food was introduced

into their immediate environment, suggesting that olfaction is necessary for the perception of distant stimuli in G. feliceps.
c) The removal of maxillary and mandibular barbels appeared to delay the final pin-pointing and ingestion of food particles by searching animals and suggested that barbels are used in the location of food in the immediate environment.
d) Animals deprived of vision were more successful at finding food than control animals, suggesting that daylight may act as an inhibitor to feeding.

Discussion

Feeding morphology

The specialised sensory structures of siluroids are believed to have evolved largely as a result of their nocturnal, benthic habits (Gosline 1973). The elaborate network of head lateral line canals, well developed olfactory rosettes and the three pairs of taste and touch sensitive circum oral barbels in Galeichthys constitute an effective nocturnal detection system for epi- and endobiontic prey (terminology after Pérès 1982).

Bardach & Atema (1971) suggest that fish taste buds have a mechano- as well as a chemosensory function. Lagler et al. (1977) state that touch sensitivity in silurid barbels arises from the nerves innervating the taste buds, which radiate to the surrounding regions and render them touch sensitive. The senses of taste and touch in Galeichthys may therefore work in unison in the selection of food before ingestion. Touch sensitivity would also compensate for the total or partial loss of vision during nocturnal foraging, or foraging in turbid environments.

While the number and size of the olfactory lamellae in fish increase with age (Kleerekoper 1969), until a certain stage of growth is reached (Pfeiffer 1963, 1965 in Yamamoto 1982), the relationship between the number of olfactory lamellae and

olfactory acuity is unclear (Pipping 1926, 1927; Wunder 1957 in Yamomoto 1982). Bond (1979) states that fish with elongated rosettes are thought to have acute powers of olfaction. The presence of an alarm substance in the epidermis of siluroids (Pfeiffer 1962), which is released on injury and serves as an olfactory intraspecific warning device, also suggests that olfaction may be acute in Galeichthys. It is not known whether the movement of water through the nasal chambers is entirely passive and dependent on forward movement of the animal, or whether active mechanisms such as cilia or accessory sacs are present. The former have been reported in ictalurids (Parker 1910, in Caprio 1982), in which olfaction was found to be a distant food-finding sense, more sensitive than the organs of taste. Caprio (1982) has since shown that olfactory and gustatory receptors, which are both chemosensory systems, detect a different but overlapping spectrum of amino acids with high sensitivity. He suggests that amino acids occurring in the prey of catfish might preferentially activate the taste system, while the olfactory sense is probably more sensitive to socially relevant stimuli. Bakhtin (1976) investigated the cellular morphology of the olfactory lining in several teleosts and elasmobranchs and described the mechanisms involved in olfactory reception and memory.

The sense of sight in Galeichthys is probably geared towards movement detection at low light intensities, in which any moving object smaller than or equal in size is a visual feeding signal and any larger moving object is a visual defensive signal. Three types of visual cells occur in teleosts, namely rods, single cones and double cones (Protasov 1970). Most pelagic fish have an abundance of rods and double cones for colour vision, while bathypelagic fish tend to have rods only. Ali & Anctil (1976) found rods and single cones in the retinas of five siluroid families indicating an adaptation to low light intensity environments, but with a retention of the ability to distinguish colour. This ability may be important to Galeichthys during daylight hours, when visual cues may be used

for adopting cryptic colouration (Protasov 1970). If the premise that eye size parallels the development of the visual capabilities of fish is correct (Protasov 1970), it must be assumed that vision in Galeichthys is fairly well developed, since their eye size approximates those of visual reef and soft substratum predators such as Petrus rupestris, Epinephelus guaza and Argyrosomus hololepidotus (Smale 1983).

While their sensory structures would equip them equally well for foraging during daylight hours or in clear water, the two main reasons for their nocturnal habit are probably to catch nocturnally active prey and to avoid predation while foraging (Sih 1987).

The robust, erectable pectoral and dorsal spines fulfill a defensive role by increasing the effective body size although they do not appear to deter predators large enough to accommodate them, and they are preyed upon by a wide variety of predatory species throughout their life-cycle. Galeichthys feliceps range over sandy and muddy substrata and probably rely on cryptic colouration and inactivity to avoid predation during daylight hours, since this environment does not provide physical shelter. They have dark, muddy coloured dorsal and lateral surfaces and lighter ventral surfaces, giving rise to obliterative shading when the incident light is from above. Obliterative shading renders objects optically flat and shadow-like (Thayer's principle), resulting in effective diurnal camouflage (Lagler et al. 1977). Galeichthys ater are darker in colour, have uniformly distributed pigmentation and probably seek refuge in caves and crevices by day. Aquarium observations have shown that both species are inactive during daylight hours. By night they are active and constantly on the move.

The obvious differences in caudal fin structure between the species gives cause for speculation as to the adaptive advantage of this phenomenon. Working on the premise that

deeply forked caudal fins are related to swimming speed, although not necessarily to swimming strength (Bond 1979), they would be advantageous for G. feliceps because of their extensive foraging areas and the need for predator evasion in a refuge-poor environment. On the other hand, G. ater forage over reefs which are smaller in extent and refuge-rich. They may have capitalised on their more stenotopic existence in this environment by decreasing the size of their caudal fin.

Diet, diet overlap, diet shift and the probability of lepidophagy

Both G. feliceps and G. ater consumed a wide variety of benthic prey. Their maximum indices of fullness (4.05% and 4.01% of body weight respectively), were comparatively low. Marais (1984) reported maximum indices of fullness of 11.5% and 10.1% for G. feliceps in the Sundays and Swartkops estuaries. These values were recorded during post-flood conditions when low salinities had driven U. africana from their burrows, making them highly accessible to predators. In addition, a maximum stomach fullness index of 18.5% was recorded in the Krom estuary. The low values obtained in this study in the marine environment are either a reflection of low prey densities, or are the result of considerable gut evacuation having occurred prior to capture.

The mean indices of stomach vacuity for G. feliceps of 14% and 3.3% in the marine and estuarine environments respectively, and 11% for G. ater in the marine environment, are indicative of a high feeding intensity. While Galeichthys are primarily nocturnal feeders, their presence in the Port Alfred commercial linefishery reveals the opportunistic nature of their feeding behaviour, since fishing occurs during daylight hours only.

Diet width is thought to vary in response to factors such as prey quality, habitat productivity and the degree of intra- and interspecific competition (Hughes 1980). While the narrow diet of G. feliceps could be ascribed to a prey-rich environment,

it might equally be a result of intense interspecific competition, particularly from benthic feeding elasmobranchs, of which there are several in the study area. The wider diet of G. ater can probably be attributed to the greater invertebrate species diversity occurring over reefs (Russell 1982). However, without quantitative data relating to prey abundance, prey selection or the degree of diet overlap between the many co-occurring species in the two environments, the above assumptions remain speculative.

Statistical quantification of diet overlap using Spearman rank correlation coefficients and the overlap measure of Schoener (1970) was unsuccessful. The data proved to be unsuitable as a result of the low number of common prey taxa at the species level, while comparisons at higher taxonomic levels would have been meaningless.

The diet shift with growth between juveniles and adults in both species probably occurs in response to several factors, including progressive loss of the ability to filter zooplankton, change in gape size enabling ingestion of larger prey taxa and migration from nursery areas.

Hoese (1966) reported scale and fin biting in juvenile Galeichthys felis Linnaeus (synonymous with Arius felis) in the Gulf of Mexico, and suggested that while this type of feeding was relatively minor, the ingested mucus might provide an important auxiliary energy source. Aquarium observations during the present study revealed that, on release from the adult buccal cavity after termination of the incubation phase, G. feliceps juveniles frequently bit the body surface and fins of adults in the tank. In addition to the energy gained in this way, it has been suggested that juvenile fish might gain immunological benefits from this habit (Hildemann 1962).

G. feliceps juveniles were also observed feeding on fins and protruding faecal matter of Liza richardsonii under aquarium

conditions. This behaviour appeared to occur in response to olfactory or gustatory stimuli rather than a visual one, since no attempt at pursuit was made by G. feliceps once the fish, presumably the source of the stimulus, moved out of their immediate environment. This argument is supported by the results of Experiment 1 above, in which it was apparent that G. feliceps was strongly chemosensorally motivated by the presence of fresh scales.

It is conceivable that in both species the sharply pointed, recurved teeth would enable the removal of scales, fins and mucus from other fish. However, it is apparent that lepidophagous fish, such as some cichlids from Lake Tanganyika (Liem & Stewart 1976) generally have a single row of large specialised teeth which facilitate the removal of scales from other fish. Similarly, Terapon jarbua, a marine scale-eating teleost (Whitfield & Blaber 1978), has an outer row of enlarged conical teeth on both jaws which are interdigitating and enable the efficient removal of scales. While it appears that G. feliceps is able to remove scales from other fish, it has not evolved specialised dentition to facilitate this habit. It is probable that the large majority of scales found in the stomachs of the estuarine caught samples were scavenged. The scales lost by other species caught in the gill net samples would have been readily accessible to G. feliceps prior to their own capture. It is also probable that G. feliceps removed scales directly from fish trapped in the nets, an opportunist feeding action which essentially amounts to scavenging.

Finally, the results of Experiment 2 above, the absence of observed visually motivated approaches towards potential hosts, and the lack of specialised dentition indicate that lepidophagy is not a reality in this species.

Habitat utilisation and resource partitioning

The absence of foraging adult G. feliceps in the Kowie River estuary gill net samples indicate that they probably prefer

deeper, marine environments. This is supported by the observation that the larger individuals caught at sea generally occur at greater depths (up to a maximum of approximately 60m) than the smaller sub-adults and juveniles which seldom occur deeper than 20 to 30m (Buxton, et al. 1984), and which forage extensively in estuaries. However, adult G. feliceps do venture into shallower water (including the mouth regions of estuaries) to forage at night, or diurnally when the water is turbid. Marais & Baird (1980), Marais (1981, 1983a & b) and Coetzee & Pool (1984) found that the bulk of G. feliceps catches in the Swartkops, Sundays, Krom and Gamtoos estuaries (south-east coast), and in the Swartvlei system (south coast) respectively, occurred in the mouth regions between the months of November and February, and that these were largely mouth brooding males. Coetzee & Pool (op cit) found that the majority of G. feliceps occurring upstream, beyond the mouth region in the Swartvlei system,were sub-adults and juveniles, a result consistent with that of this study. Estuaries therefore form an extension of the inshore habitat for G. feliceps juveniles and sub-adults, and the extent to which they utilise estuaries is largely dependent on the prevailing turbidity, as suggested by the data of Marais (1984) for the Swartkops, Sundays, Krom and Gamtoos estuaries. The Swartkops estuary produced the lowest cpue for Galeichthys and was the least turbid, while the Gamtoos estuary was the most turbid and yielded the highest cpue. However, G. feliceps are unable to tolerate salinities much below 8 ppt. (Whitfield et al. 1981; Bennett 1985) and are thus prevented from foraging in estuaries during flood conditions, when food is often abundant. Estuarine predators of G. feliceps such as Argyrosomus hololepidotus and Elops machnata (Marais 1984) and Platycephalus indicus (this study) probably also influence their estuary utilisation patterns.

Galeichthys ater are restricted to reef habitats and do not occur in estuaries. As with G. feliceps, there is an increase in the size distribution of G. ater, in hook and line catches, with increasing depth. Juvenile G. ater utilise near-shore,

sub-tidal reefs as nursery areas at the termination of the mouth brooding phase, where they feed prolifically on amphipods and isopods, before moving to deeper habitats.

A preliminary feeding study on the Galeichthys species occurring off the Transkei and Natal coasts suggested that it forages over both hard and soft substrata. The warm waters of the east coast are home to a wide variety of sharks, many of which prey on Galeichthys, including five carcharhinid species, Carcharinus limbatus, C. obscurus, C. brevipinna, C. leucas and C. amboinensis, the spotted ragged tooth Eugomphodis taurus, three hammerheads, Sphyrna lewini, S. zygaena and S. mokarran, the tiger, Galeocerdo cuvier and the great white, Charcharodon carcharias (J. Cliff, Natal Sharks Board, pers. comm.). This species is largely inactive during daylight hours when it remains within the confines of caves and other sources of refuge offered by reefs (Van der Elst 1981; M. Griffiths, Dept. Ichthyology & Fisheries Science, Rhodes University, pers. comm.). While this diurnal inactivity may be a predator evasion tactic, it is more probably due to their largely nocturnal habit. While this species appears to utilise both both reef and soft substratum environments, it does not frequent estuaries, as was evidenced by its absence from the gill net surveys of Wallace (1975), conducted in several east coast estuaries. It is probable that the southern distribution of this species is limited by water temperature.

Grossman (1982) has questioned whether resource partitioning is necessary for co-existence in stochastic communities, and has, along with other authors (Moyle et al. 1982) emphasised the importance of long-term monitoring in order to determine the nature of the community under investigation. Since the duration of this study was not long enough to allow such an evaluation, it was impossible to demonstrate whether the resource partitioning observed between G. feliceps and G. ater was a real (permanent) phenomenon. However, according to the theory of island biogeography (MacArthur & Wilson 1967), K-

selected species assemblages are a characteristic of stable environments. If the presence of K-selected species can be relied upon as an environmental indicator, the near-shore habitat along the eastern Cape coast may be assumed to be a deterministic one. Therefore, resource partitioning may well have played an important role in shaping community structure in this region.

Since the large majority of ariid species world-wide appear to forage over soft sediments (Taylor & Menezes 1977; Taylor & Van Dyke 1981; Jayaram & Kailola 1983), it seems logical to assume that this is their preferred habitat type. It was surprising therefore that G. ater chose to forage almost exclusively over reef environments. Either this species was competitively excluded from the preferred habitat during the course of its co-evolution with G. feliceps, or it was pre-adapted to reef environments prior to its sympatry with G. feliceps.

The evolutionary significance of interspecific competition (and by inference, resource partitioning) has been the subject of much debate (e.g. MacArthur 1972; Schoener 1974, 1983; Connell 1980, 1985; Roughgarden 1983; Davic 1985; Maurer 1985). While character displacement (Brown & Wilson 1956 in Price 1975), or habitat shift (Schoener 1974) invariably results when two normally allopatric, morphologically and behaviourally similar species find themselves in sympatry, it has not been conclusively shown that such character displacement may subsequently become genetically fixed (Connell 1980). In the absence of this proof, Connell (op cit.) argues that interspecific competition should not be viewed as a mechanism which directs co-evolution.

Mayr (1970) has argued that co-evolution of sympatric, congeneric species over vast time periods has often resulted in a high degree of resource partitioning. This led to the initial speculation that resource partitioning between the two morphologically and behaviourally similar Galeichthys species

was likely to be intricate. However, while morphological similarity resulted in similar feeding modes and prey taxa in Galeichthys, their separation by habitat preference isolated them from each other to the extent that in terms of range overlap, they effectively existed in allopatry. It is likely, however, that there may be a certain degree of aggressive competitive interaction in the areas abutting reefs, where both species probably forage. Hixon (1980) found this to be the case between overlapping populations of two predominantly allopatric California surfperches, Embiotoca lateralis and E. jacksoni (Embiotocidae). Largely as a result of their morphological and behavioural similarity, the diets of these two allopatric species were also very similar and resulted in considerable competitive interactions for food and territories in sympatry, at the interface of their respective habitat ranges. Using manipulative experiments Hixon (op cit.) demonstrated that E. lateralis competitively excluded E. jacksoni from the preferred foraging environment, namely the productive shallow reef areas.

The extreme nature of resource partitioning demonstrated by the two Galeichthys species, namely habitat separation, is surprising in the light of the great many ariid species occurring in apparent sympatry elsewhere in the world. For example, many of the estimated 77 species which occur in the Indo-Pacific Archipelago (Wongratana et al. 1974), have overlapping distributional ranges. Although little is known about the feeding habits of the majority of species, it is generally stated that they feed predominantly on invertebrates and small fish, and that in many fisheries several species may be caught simultaneously, using the same gear (Wongratana et al. 1974; Taylor & Menezes 1977; Taylor & Van Dyke 1981; Jayaram & Kailola 1983). Araújo (1984) did not detect resource partitioning of any nature amongst three ariid species in a Brazilian coastal lagoon and suggested that food was not a limiting factor within their common habitat. However, he did find significant differences in feeding-associated morphological features such as gape size, eye diameter and

intestine length, suggesting that food overlap might decrease if food became less abundant, a phenomenon that has been demonstrated by many authors (see Ross 1986 for review). While detailed feeding studies over long periods of time invariably reveal the presence of resource partitioning, it is equally clear that the majority of species feed opportunistically and that in times of food abundance considerable diet overlaps will occur, particularly amongst morphologically similar congeneric species. The rigid and apparently permanent habitat separation demonstrated by G. feliceps and G. ater in this study is therefore unusual, although direct observations of their foraging behaviour may reveal considerably more interaction between them than their diets suggest.

In conclusion, it was apparent that the feeding associated morphologies of the two species were highly similar. The taste and touch sensitive circum-oral barbels, elaborate head lateral line network and well differentiated olfactory rosettes clearly indicated that they were adapted for benthic foraging in conditions of low light intensity. While the major food taxa of the two species were identical, species level identification of prey revealed a rigid partitioning of food and, consequently, of space between them. Galeichthys feliceps foraged entirely over soft sediments while G. ater fed predominantly over reefs and marginally over soft sediments. The wider diet of G. ater was probably attributable to a greater species diversity over reefs, although this was not quantitatively demonstrated.

CHAPTER 3 - REPRODUCTION

Introduction

An outstanding feature of fish reproduction is the immense range of fecundities exhibited within the group as a whole. At the one extreme there are certain elasmobranchs (e.g. Squalus spp.) which produce between two and three young every second year (Gilbert & Gilbert 1980), and at the other there are teleost pelagic spawners such as the ocean sunfish (Mola mola), which produce up to 28 million eggs per annum (Lagler et al. 1977).

Mortality in fish populations is characteristically high during egg and larval stages and in an evolutionary sense the number of eggs produced by a fish is probably linked to the expected mortality between spawning and recruitment into the parent population (Nikolsky 1969; Cushing 1975; Sissenwine 1984). Two major factors influencing survival during early ontogenetic development in fish are availability of energy for growth and vulnerability to predation. Broadcast spawners characteristically produce large numbers of small eggs with an abbreviated embryonic phase and a prolonged, free-floating, energy-gathering larval stage. Larval survival is largely dependent upon chance encounters with food and passive avoidance from predators, and is characteristically low. As egg size and degree of parental care in fishes increases, fecundity tends to decrease (Lagler et al. 1977). This is particularly well demonstrated in the gradation of reproductive guilds (sensu Balon 1975a, 1981a,b, 1984) from egg hiding, egg guarding, external egg bearing (e.g. oral gestation), to internal bearing in the form of viviparity. The trend is for greater amounts of energy to be invested into fewer young, each with a higher chance of survival through to recruitment into the reproductively active adult population (Oppenheimer 1970).

Studies of reproduction in ariids (see Rimmer & Merrick 1983 for review, also Mansueti & Hardy 1967; Jones et al. 1978; Lara-Domínguez et al. 1981; Menon 1984; Mishima & Tanji 1985; Rimmer 1985a, 1985b; Reis 1986; Coates 1988; Yánez-Arancibia & Lara-Domínguez 1988) have demonstrated that they are a highly K-selected group. The largest egg diameter reported for the family is 20mm (Rimmer & Merrick op cit.), a size unsurpassed amongst teleosts (Atz 1958), while their average fecundity at approximately 60 eggs per annum (Rimmer & Merrick op cit.) is amongst the lowest exhibited amongst teleost fishes.

The specialised reproductive modes referred to above are thought to have evolved in response to stable, predictable environments (Duellman 1989), where properties such as rapid population growth are not a prerequisite for survival. In the fisheries context the resilience of a population to exploitation is of over-riding importance, both in terms of the economics of the fishery and the survival of the stock. Species that are r-selected generally have high fecundities and rapid population regeneration rates. Their high growth potential renders them particularly resistant to the effects of fishing pressure and the sustainable yields exhibited by fisheries for these species are essentially supported by surplus production (Garrod & Horwood 1984).

The K-selected (MacArthur & Wilson 1967) or precocial (Balon 1979) species on the other hand tend to have low fecundities and generate little surplus production. They exhibit slow population growth rates and as a result they are highly sensitive to environmental perturbations and extremely vulnerable to over-fishing (Adams 1980). Examples of their vulnerability include the destruction of cichlid populations after introduction of the Nile perch into Lakes Kyoga and Victoria (Ribbink 1987), the rapid and considerable decline in populations of elasmobranchs (Holden 1977; Compagno In press) and marine mammals (Allen & Kirkwood 1988) following the initiation of intensive fisheries for them.

Considering the above, and the fact that the two ariid species formed a considerable component of the fishery at Port Alfred, there was a need to assess their reproductive potential and, hence, their vulnerability to fishing pressure.

The models used in this study to assess the effects of exploitation on the population dynamics of the two species (see Chapter 6), were initially developed for the cod, herring and plaice stocks of the North Atlantic (Beverton & Holt 1957). Although the relationship between the numbers of spawners and recruits was poorly understood in these populations it was assumed that because of their extremely high fecundity, recruitment variability would not be limiting to population growth. In the formulation of the models, recruitment was therefore assumed to be constant and independent of stock size (Beverton & Holt op cit.). Yield in the fishery was calculated as a function of fishing mortality rate and the age of entry into the fishery (Smith 1988). The only reproductive information required by the models was the size at sexual maturity.

When considering the exploitation of strongly K-selected species, however, recruitment is likely to be intimately linked with the size of the reproductively active parent stock. Thus the assumption of constant recruitment theoretically does not hold for such populations. As recruitment was not determined for the two populations under study, the conventional yield-per-recruit model was still the best available method for determining their population responses to exploitation.

In the light of the model's limitations it was anticipated that a thorough knowledge of the reproductive biology of the two species would be of considerable importance when interpreting the yield-per-recruit curves at the end of the study.

The large egg size, low egg number and paternal mouth-brooding habit of G. feliceps has been commented on by several authors

in the literature (Smith 1961; Marais & Baird 1980; Day et al. 1981; Van Der Elst 1981; Coetzee & Pool 1984; Taylor 1986; Marais & Venter 1987). These studies were, however, incomplete and inadequate to meet the above requirements.

This chapter represents the first detailed investigation into the reproduction of G. feliceps and G. ater using data collected over a three year period, and covers the following aspects: Spawning seasonality, sizes at sexual maturity, fecundity, spawning behaviour and differential reproductive energy investment by the sexes. Two other important aspects of reproduction, the early ontogeny and duration of mouth-brooding, are investigated in Chapter 4 for G. feliceps.

Materials & Methods

Biological samples obtained from the commercial fishing wharf were collected over three years and processed on a monthly basis. The following information was recorded: body, gonad, fat and liver mass, fork length, sex, gonad maturity, egg size and egg number.

Sizes at 50% sexual maturity were determined using an accumulative technique in which the frequency of mature gonads encountered during the spawning season was plotted against size class. The size class in which at least 50% of fish exhibited mature gonads was adjudged to be the size at 50% maturity, and was determined independently for the sexes.

Gonadosomatic (GSI) indices were used to determine the period and frequency of spawning, and were calculated as a function of body weight as follows:

$$GSI = GONAD\ MASS \times 1000 / BODY\ MASS$$

Hepatosomatic (HSI) and abdominal fat-somatic (FSI) indices were determined in order to follow trends in energy accumulation and expenditure. For the calculation of these two indices a correction factor for gonad mass was incorporated in order to avoid masking of the trends. The formulae were as follows:

HSI or FSI = LIVER or FAT MASS X 1000 / (BODY MASS - GONAD MASS)

As males do not feed while mouth-brooding (see Chapter 4), the condition factor (CF) was used to determine the extent of the weight loss that occurred during this period. Condition factors for females were calculated for comparative purposes. The condition factors were calculated as follows:

CF = (BODY MASS - GONAD MASS) x 1000 / (FORK LENGTH ^ b)

where b = the exponent derived from the natural log regression of length against weight (3.08 for G. feliceps and 3.04 for G. ater).

The plots of mean monthly indices were used to exhibit seasonal trends. The abscissa of all plots began and ended with the months of July and June respectively in order to avoid graphic interruption of the spawning period.

In order to detect energy utilisation trends in mouth-brooding individuals which are absent from commercial catches, the above indices were calculated independently for mouth-brooding G. feliceps males captured in the Kowie estuary between October and March each year using gill nets. Mouth-brooding G. ater males could not be captured and the physiological effects of mouth-brooding in this species could therefore not be determined.

Adult male fish which were caught in the fishery during the usual mouth-brooding season were individuals which for some

reason had not spawned, possibly due to poor condition or through failure to procure a mate. If a certain proportion of the reproductively active male population adopted sneaking as an alternative reproductive strategy they would also be caught during this time.

All indices were determined only for individuals equal to or larger than the size at 50% sexual maturity.

In an attempt to explain why males and not females are the mouth-brooders in ariids, a reproductive energy budget was drawn up for G. feliceps. Using adiabatic bomb calorimetry the energy content (Kj/g) of mature yolky eggs, hyaline eggs, testes, fat, flesh and liver tissue were determined. This data enabled the calculation of the approximate reproductive energy investment for the sexes. Similar sized males and females were used in the analyses.

In ariids two types of eggs are released at spawning. The few large, yolky eggs which are subsequently fertilized by the male are accompanied by large numbers of small, hyaline eggs of unknown function (Rimmer & Merrick 1983). In the determination of fecundity the mean number of yolky eggs spawned per annum was used. To determine whether fecundity increased as a function of body size the mean number of mature eggs was plotted against fork length. Relative fecundity (RF) was determined in order to enable comparisons to be drawn between the two species and was calculated as follows:

$$RF = \text{GONAD MASS} / (\text{BODY MASS} - \text{GONAD MASS})$$

The mean number of hyaline eggs and their total average weight relative to the yolky eggs in the ovaries was also determined. It was hoped that the determination of the amount of energy they contained might reveal something about their possible function.

Mouth-brooder buccal cavity volume was measured in order to reveal whether males were physically able to carry some or all of the eggs from one female, or whether they were able to carry the egg compliment from more than one female. This was necessary since it was found that mouth-brooding males invariably spat out some or all of their brood when they became entangled in gill nets, and an accurate assessment of the number of young they incubated could not be made. Buccal volume was determined using mouth-brooding males caught in gill nets. The buccal volume in the male is increased by lowering the hyoid complex during mouth-brooding. As the buccal cavity remained distended after death it was a simple matter to pour liquid plaster-of-Paris into their mouths. After the castes had dried they were dissected out and shaped using a file. This was to remove plaster-of-Paris where it had penetrated between the gill arches. The volumes of the castes were determined by immersion into a calibrated container filled with water.

Secondary sex characters were observed in both species and were briefly described. Although spawning was not observed in either species, their proposed spawning behaviour was speculated upon on the strength of the secondary sex characters and the reproductive data.

Results

Three secondary sex characters were noted in G. feliceps and G. ater, while a fourth was peculiar to G. ater.

a.) The pelvic fins of adult females were significantly longer and wider than those of males (Table III). It was envisaged that they played an active role during spawning. Captured ripe-running females were sometimes seen to splay their pelvic fin rays and to hold the fins erect, forming a cup around the vent. It is possible that the eggs, which are adhesive once spawned, are held in the pelvic fin cup whilst the male fertilizes them.

Table III. Student t-tests demonstrating significant sex-related differences in the lengths and widths of pelvic fins in G. feliceps and G. ater.

	Males			Females					
	n	mean	sd	n	mean	sd	df	t-test (95%)	sig dif (Y/N)
				G. FELICEPS					
PELVIC LENGTH	23	10.530	1.496	40	14.261	1.245	61	-4.9699	YES
PELVIC WIDTH	23	8.609	0.951	40	12.719	1.541	61	-6.0219	YES
				G. ATER					
PELVIC LENGTH	25	10.927	0.902	48	13.554	1.985	71	-3.5503	YES
PELVIC WIDTH	25	8.879	0.913	48	12.123	1.844	71	-4.5897	YES

b.) In males, the pharyngeal and palatine tooth-patches became completely embedded in a film of dense, congealed mucus during the mouth-brooding phase. Teeth on the pre-maxilla and dentary were free of this mucus and remained exposed.

c.) The shape of the cleithrum in sexually mature individuals was different for males and females. The posterior margin of the post-humeral process was rounded in females and angular in males (Fig. 13).

d.) Galeichthys ater females developed a fatty growth on their pectoral spines during the spawning season, which was not observed in the females of G. feliceps or on males of either species (Plate III). Males and females of both species are able to produce sound by moving their pectoral spines rapidly backwards and forwards. The sound is produced in a stridulatory manner when the pectoral spine condyle moves across the ridged surface of the socket in the pectoral girdle (pers. obs.).

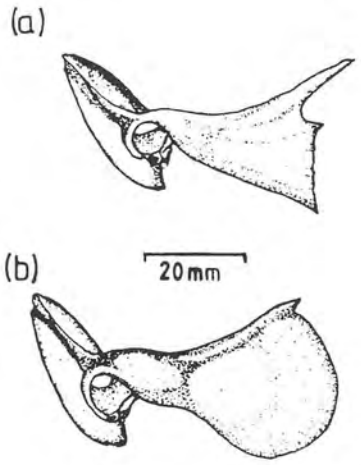


Figure 13. Left lateral view of a) male, and b) female pectoral girdle (pectoral fin removed), demonstrating the sexual dimorphism in the shape of the post-humeral process of the cleithrum.

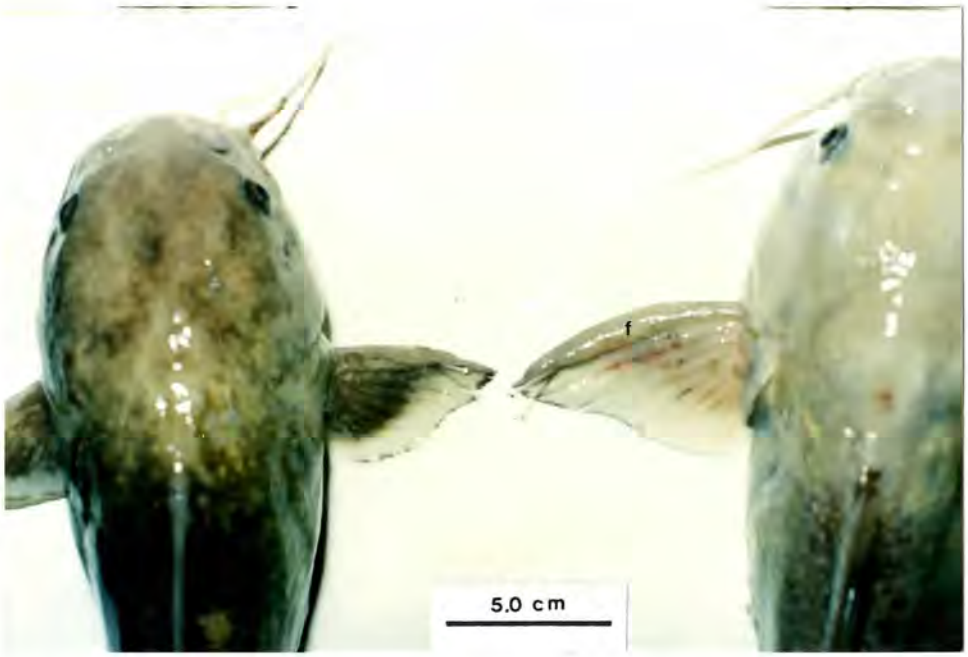


Plate III. Dorsal aspect of male (left) and female (right) G. ater showing the fatty growth (f), on the pectoral spine of the latter during the spawning season.

Gonad description

The following macroscopic description is devoted to the seasonal changes occurring in the gonads of sexually mature fish. Gonadal development was identical in the two species and a single description suffices for both. The seven-stage macroscopic gonad maturity scale used is a modification of the six-stage scale used by Nikolsky (1963).

Stage 1 - Immature

The testes were thin, thread-like and translucent, extending from the vent anteriorly approximately half way to the posterior edge of the swim bladder. The ovaries were distinguished from the testes only by a gradual thickening at their distal end. Eggs were not visible to the naked eye.

Stage 2 - Quiescent/Recovering

Testes were thin, and flattened in cross section, creamy-beige in colour and were attached along their entire length, both to one another and to the dorsal lining of the coelomic cavity, by a medial mesorchium. The outer lateral edges had a frilled appearance. The stage 2 recovering testes were similar in appearance, although considerably longer, extending almost to the swim bladder. The ovaries, distally lobate in the region of the developing eggs, were translucent and attached to the dorsal body wall by a mesovarium. The two ovaries unite proximally to form a single oviduct. The distally situated eggs (± 2mm-3mm in diameter) were pale orange in colour and interspersed with two smaller egg-types, some pale yellow and some creamy-white, both approximately 1.5mm in diameter. Proximally, the ovarian wall bore masses of very small (± 0.2mm-0.3mm) white eggs. The walls of Stage 2 recovering ovaries were thickened and opaque.

Stage 3 - Developing

The testes were longer, extending all the way to the swim bladder, pinkish in colour and semi-circular in cross section with the ventral surface being rounded. They were proximally

thin in the region of the long deferent duct (Loir et al. 1989), with only the distal half of the testes being thickened. The outer lateral edges were still frilled in appearance. The lobate distal region of the ovaries contained yolky eggs of approximately 4mm-6mm in diameter.

Stage 4 - Active

The testes had a reddish tinge. The proximal third of the testes remained underdeveloped and more deeply reddened than the distal two thirds, which were swollen and approximately 9mm in width (Plate IVa). The ovaries were greatly enlarged and occupied approximately 50% of the body cavity. The ovarian walls had stretched and become more translucent making the large (± 8mm-9mm) yolky eggs and the small, creamy-white eggs, termed hyaline eggs (Rimmer & Merrick 1983), interspersed between them clearly visible. The follicular blood vessels were prominent against the yellow yolk of the developing eggs (Plate IVb).

Stage 5 - Ripe

The testes had lost their redness and were pale and translucent (Plate IVa). Distally the girth of each testis had increased to a width of approximately 12mm. When incised they released colourless milt. The ovaries were greatly enlarged and contained eggs of approximately 11mm-14mm in diameter (Plate IVb). Females with ripe ovaries could be identified externally by their distended ventral abdominal wall.

Stage 6 - Ripe-running

Testes in the ripe-running condition were completely translucent and on application of slight pressure released colourless milt. Ripe-running ovaries were identified as those in which the eggs had been released from their follicles (stratum germinosum), (Plate IVc). The yolky and hyaline eggs were easily extruded upon application of slight pressure to the abdominal wall. A plug of small hyaline eggs (each ± 0.7mm in

diameter) was extruded first, and were followed by the yolky eggs (± 13mm), interspersed with larger hyaline eggs (± 1.8mm).

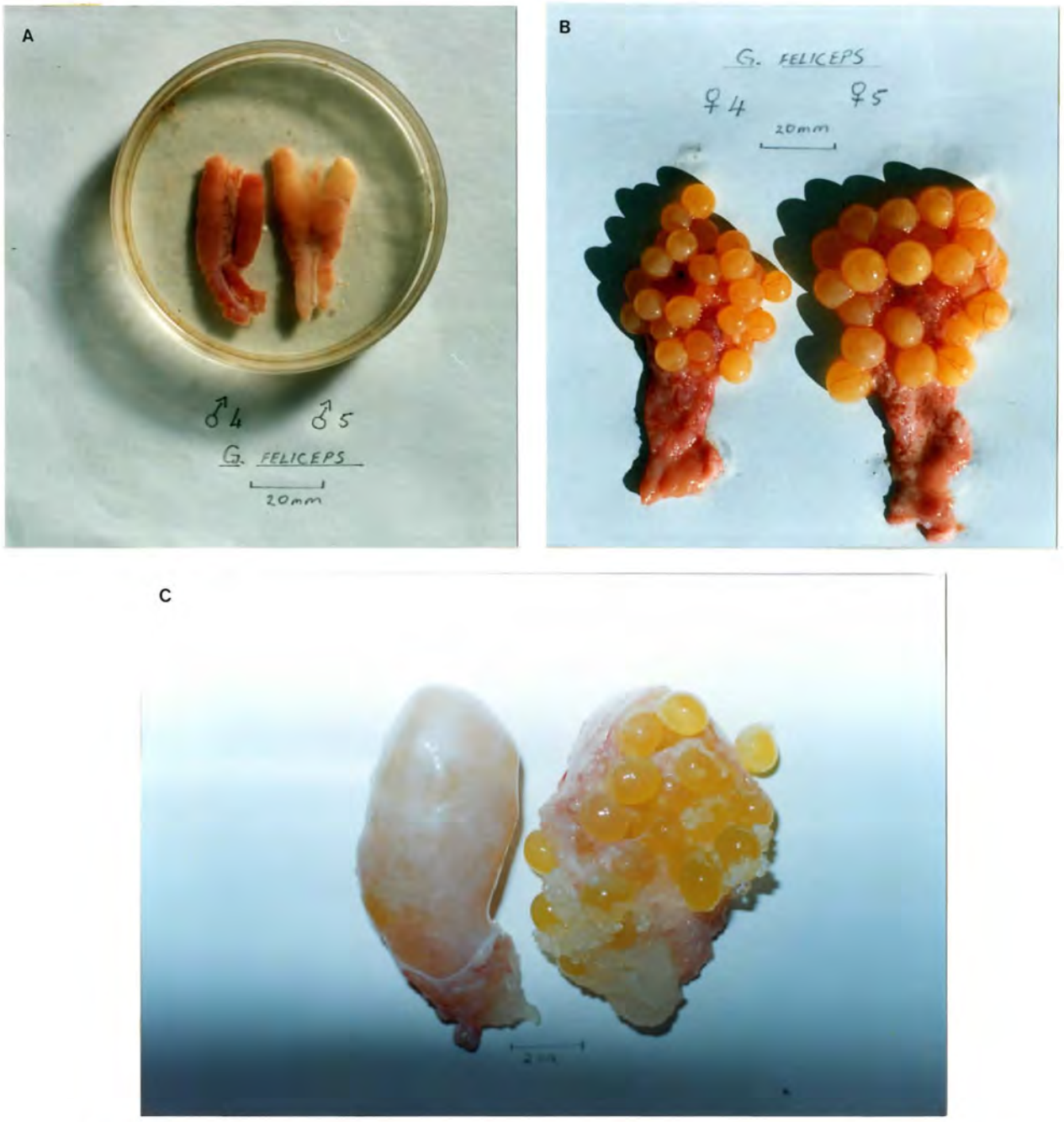


Plate IV. G. feliceps gonads in (a) stage 4 and 5 testes, (b) stage 4 and 5 ovaries, (c) stage 6 ovary showing loose ripe and hyaline eggs after release from the follicles.

Stage 7 - Spent

Spent testes were deeply reddened and flaccid. Ovaries were similarly flaccid. Distally, amongst the empty follicles, small, pale yellow eggs of approximately 2.5mm in diameter were visible. These probably represented the following season's compliment of yolky eggs. No hyaline eggs were visible to the naked eye.

Four different egg sizes were present in ripe ovaries. Situated distally the large (± 13mm in diameter), orange-yellow yolky eggs were the most obvious. Closely associated with them were a similar number of small (± 2.5mm) pale yellow, immature yolky eggs. An abundance of hyaline eggs (± 1.75mm) also occurred amongst the yolky eggs. Hyaline eggs of a distinctly smaller size class (± 0.7mm) were distributed throughout the mid- and proximal regions of the ovary. They were particularly densely distributed on the ovigerous folds of the tunica albuginea in the vicinity of the oviduct. The sizes and colours of the different egg-types are presented in Table IV.

Table IV. The position, size and colour of the egg-types found in Galeichthys feliceps and G. ater ovaries.

Egg type	Position in ovary	Colour	Diameter (mm)	sd
small hyaline	proximal	white	0.69	0.15
large hyaline	distal	white	1.75	0.19
immature yolky	distal	pale yellow	2.63	0.21
ripe yolky	distal	orange-yellow	13.19	0.44

Sizes at sexual maturity

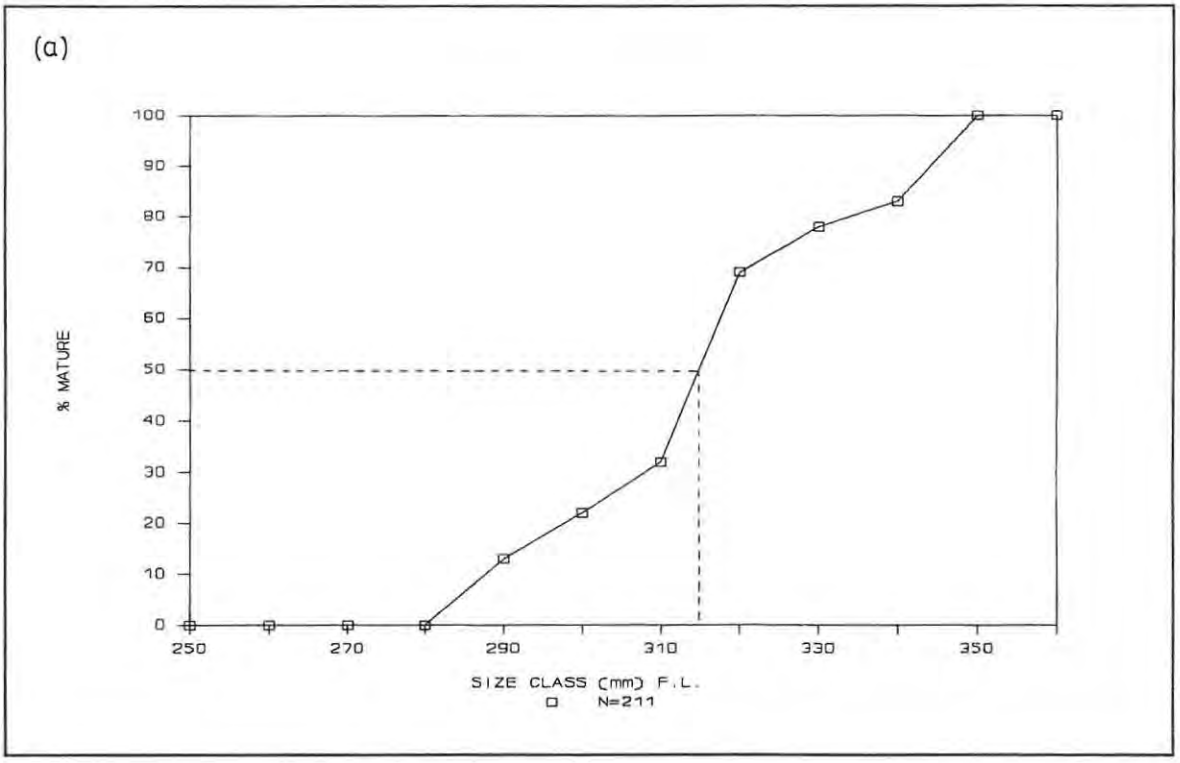
G. feliceps males and females reached 50% sexual maturity at approximately 315mm and 295mm (FL) respectively (Fig. 14). In G. ater 50% maturity was reached at approximately 235mm in both sexes (Fig. 15). Galeichthys ater males did not demonstrate 100% maturity at any size. This would appear to suggest that all individuals did not spawn each year. A similar phenomenon was observed amongst the larger female size classes.

Spawning seasonality

The spawning season was determined from the monthly gonadosomatic indices (GSI's) and revealed that spawning occurred once a year in both species. In G. feliceps gonads reached a peak in development in September and spawning occurred between September and December (Fig. 16). In G. ater spawning occurred between August and October (Fig. 17).

Seasonality of energy reserves associated with reproduction

The mean monthly fat-somatic indices (FSI's) demonstrated distinct sex-specific trends. In males, fat deposits were accumulated during autumn and winter prior to the spawning season (Fig. 18). In females, fat reserves were accumulated during summer after spawning and declined steadily during the winter months (Fig. 19).



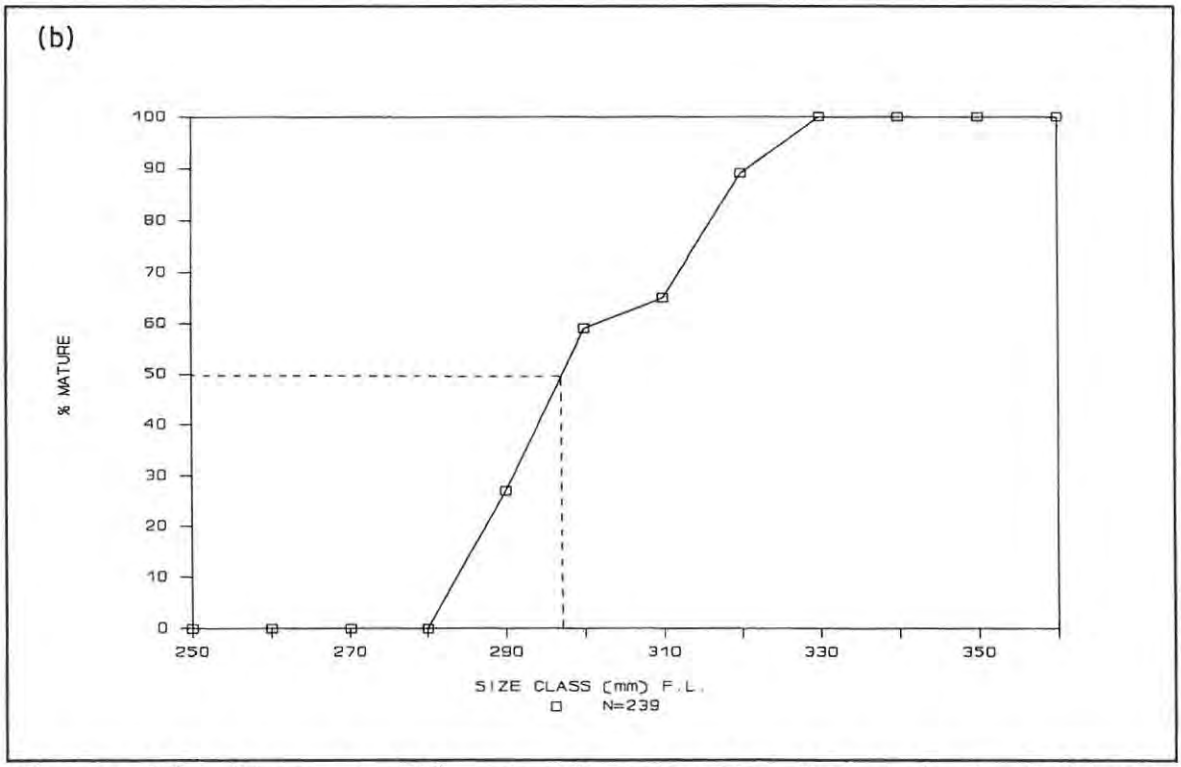
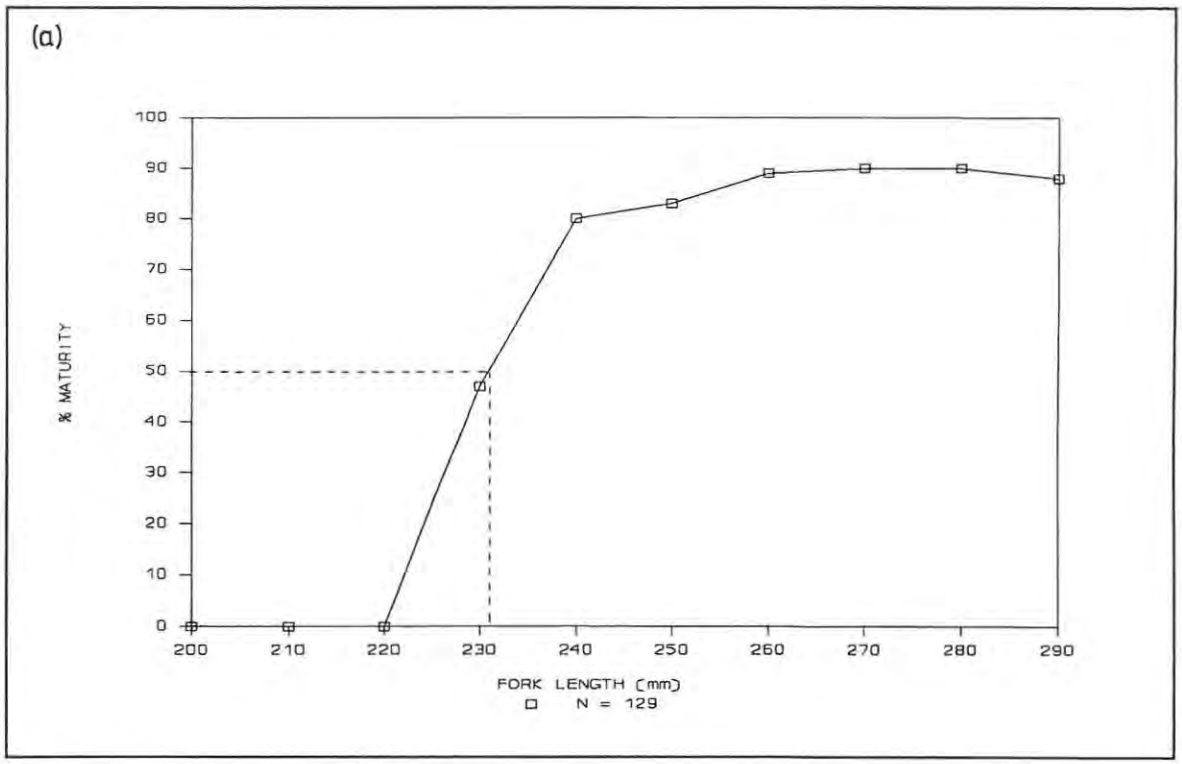


Figure 14. Size at 50% sexual maturity for (a) G. feliceps males (± 315mm) and (b) females (± 295mm).



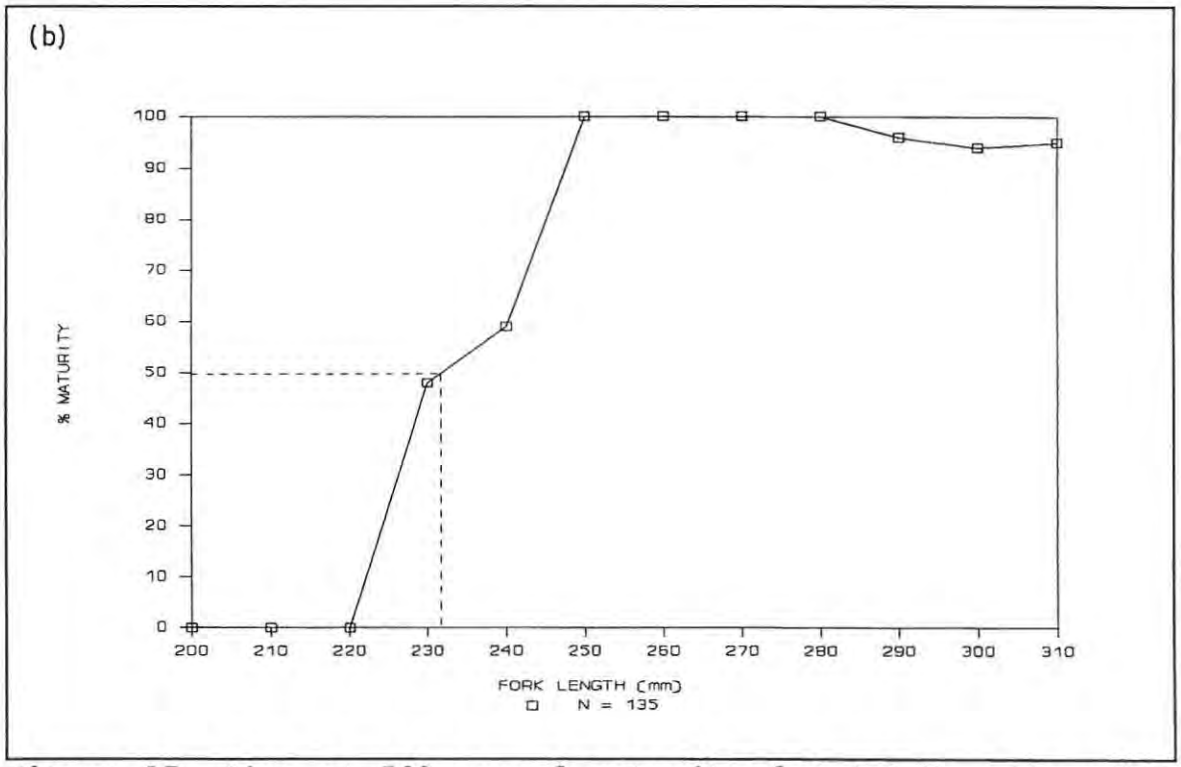
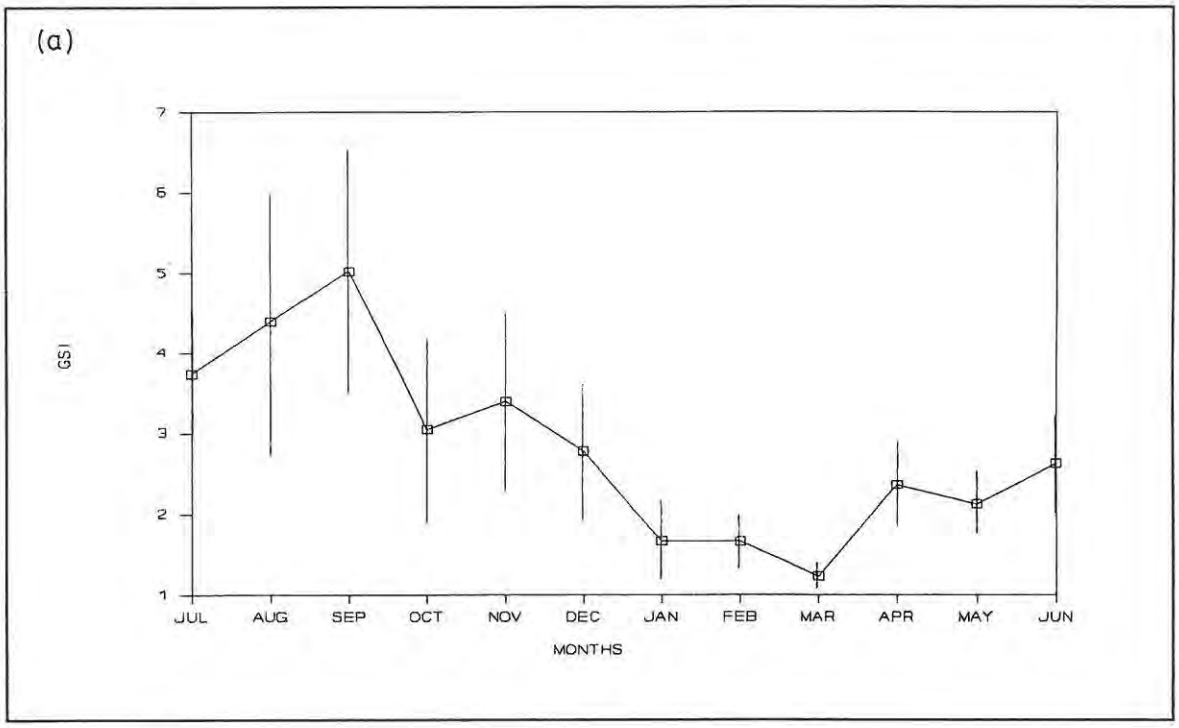


Figure 15. Size at 50% sexual maturity for (a) G. ater males (± 235mm) and (b) females (± 235mm).



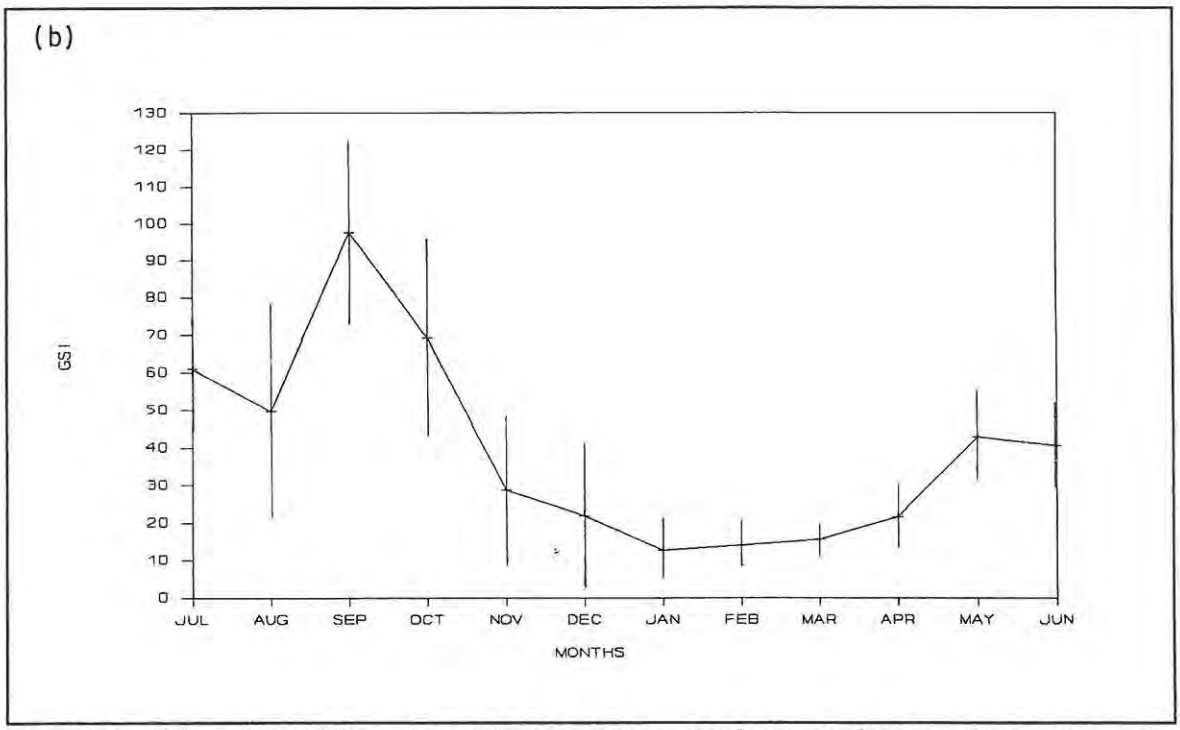


Figure 16. Monthly gonadosomatic index values for (a) G. feliceps males and (b) females, demonstrating peak gonadal development during September. Vertical bars represent 1 SD.

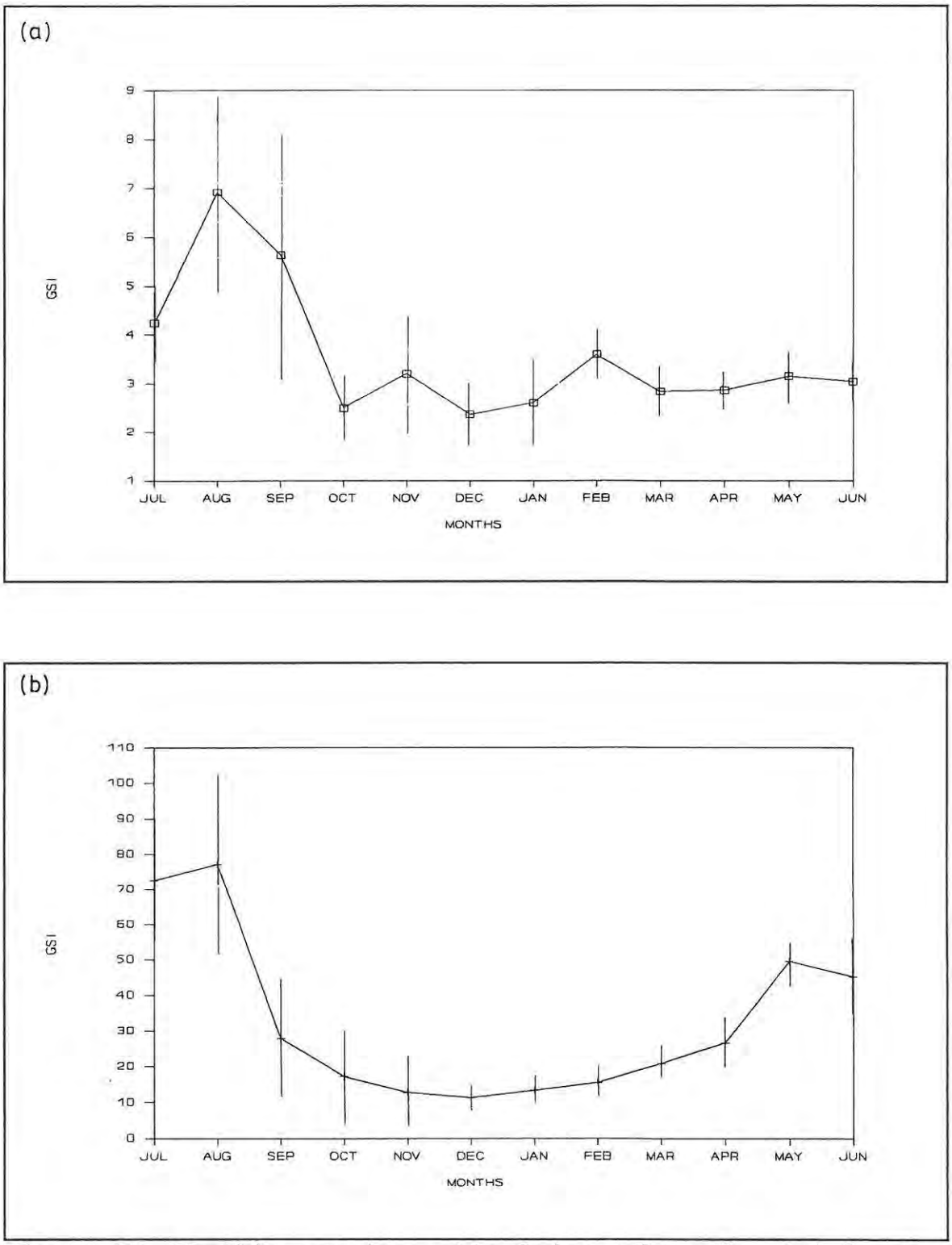
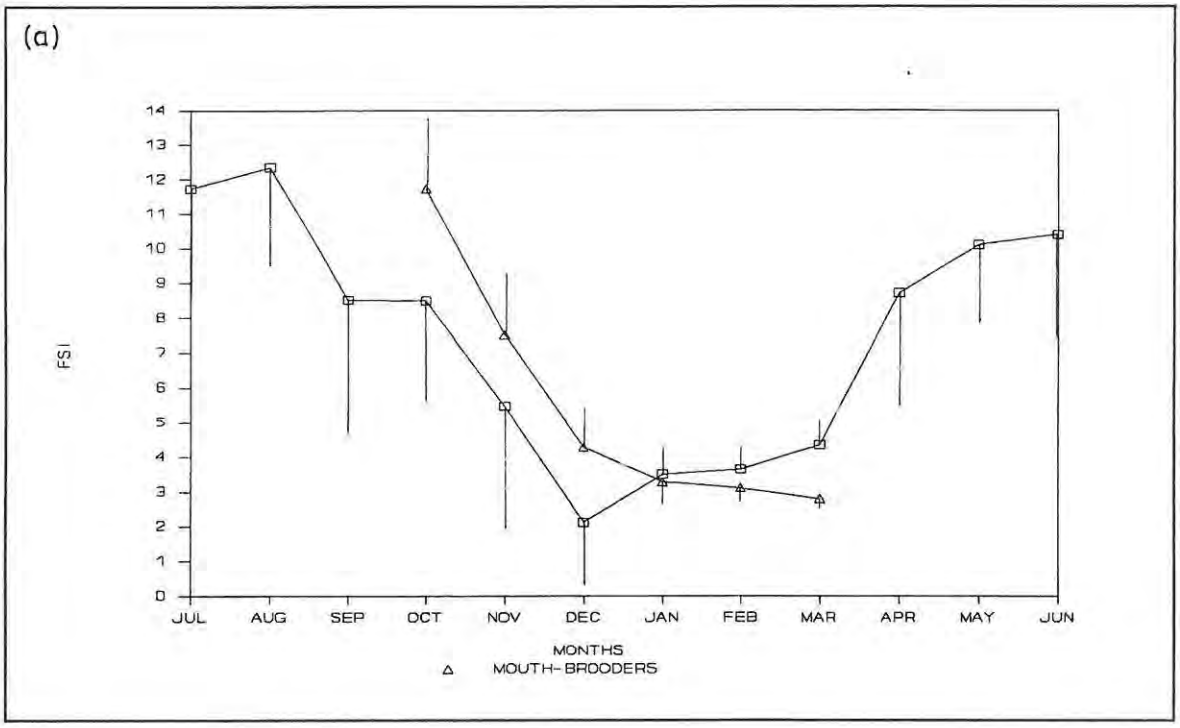


Figure 17. Monthly gonadosomatic index values for (a) G. ater males and (b) females, demonstrating peak gonadal development during August. Vertical bars represent 1 SD.



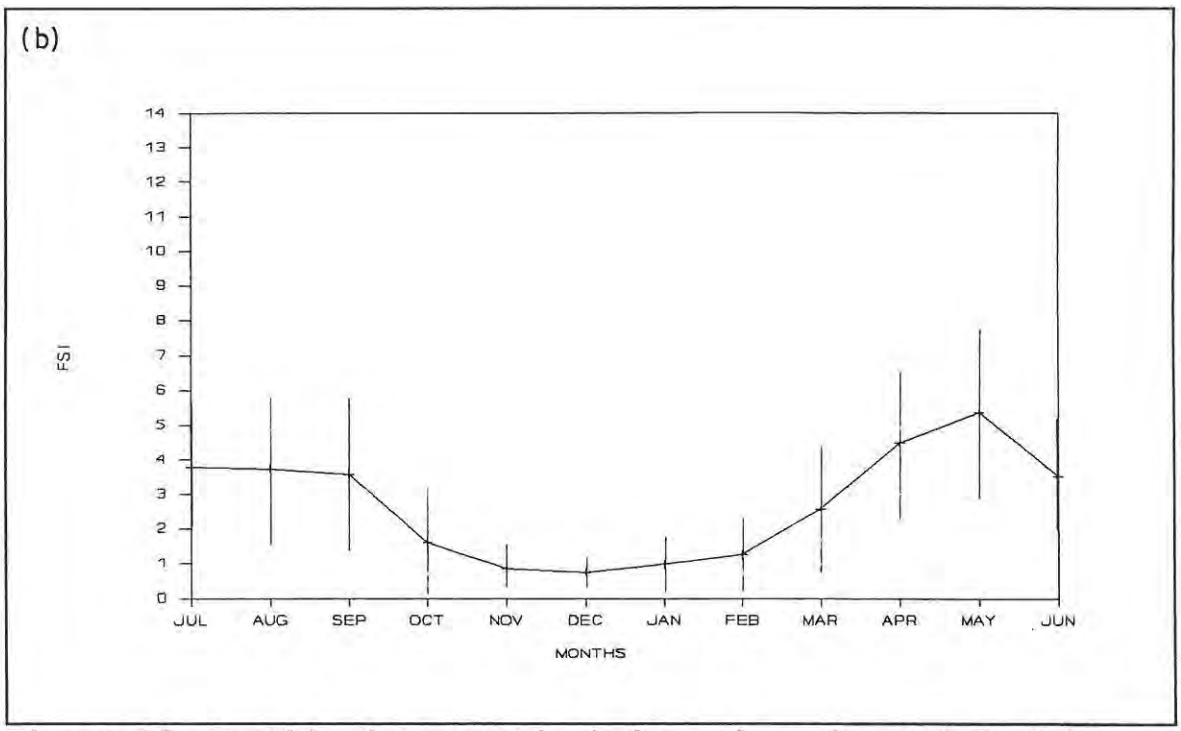


Figure 18. Monthly fat-somatic index values for (a) G. feliceps males (mouth-brooders plotted separately). Vertical bars represent 0.5 SD, and (b) females. Vertical bars represent 1 SD.

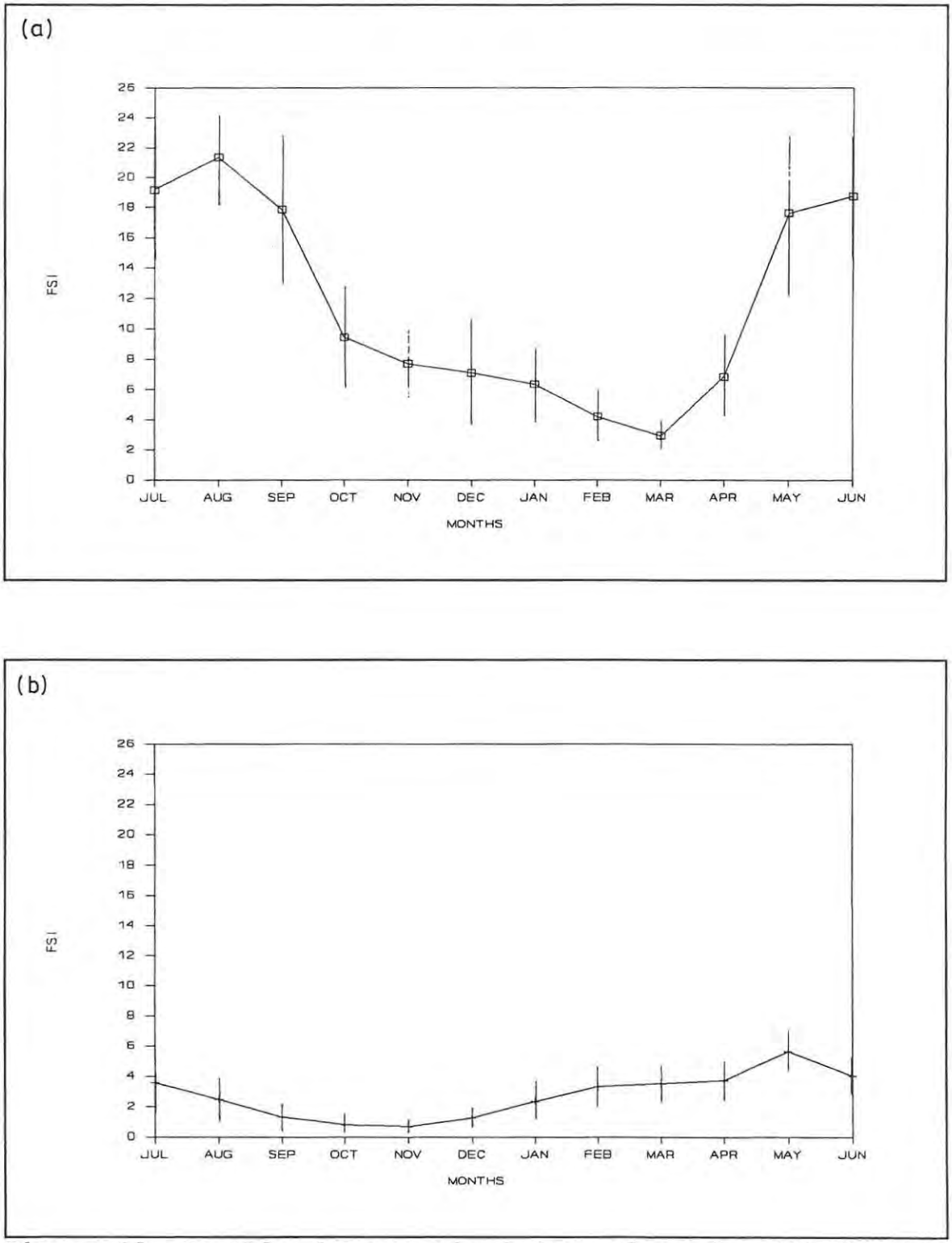
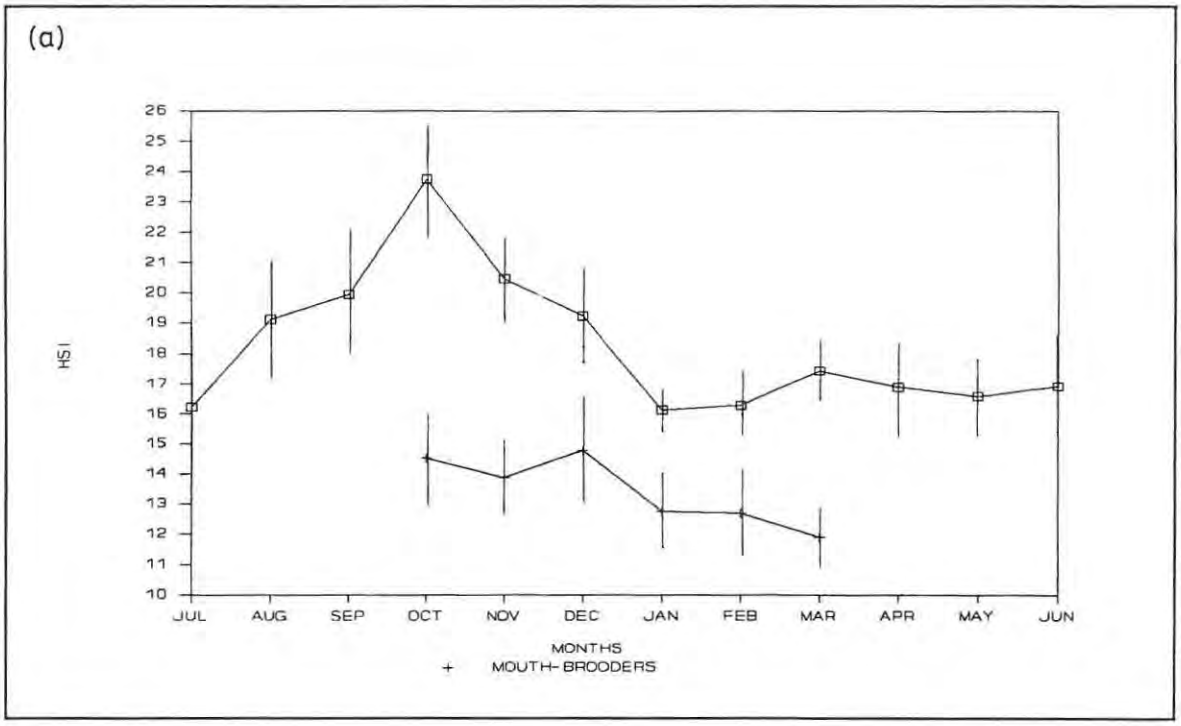


Figure 19. Monthly fat-somatic index values for (a) G. ater males and (b) females. Vertical bars represent 1 SD.

The mean monthly hepatosomatic indices (HSI's) for G. feliceps males exhibited a peak during September and October, at the onset of spawning. The HSI's for estuarine caught mouth-brooding individuals demonstrated that liver mass reached a low point at the culmination of the buccal incubation period (Fig. 20a). Mouth-brooding G. ater males were not captured and the monthly HSI's therefore do not reflect a marked decline until January when individuals which had completed their mouth-brooding began to be caught in the fishery again (Fig. 21a). The HSI's for females did not fluctuate substantially (Figs. 20b & 21b).

Condition factors for the sexes followed much the same trend as the fat and hepatosomatic indices. In G. feliceps male body condition declined markedly during the mouth-brooding period (Fig. 22a). Females reached peak condition in May prior to the onset of gonad maturation, although their condition did not fluctuate markedly (Fig. 22b). Mouth-brooding G. ater males were not captured and the monthly condition factor curve is therefore not an accurate reflection (Fig. 23a). G. ater females did not vary markedly in condition (Fig. 23b).



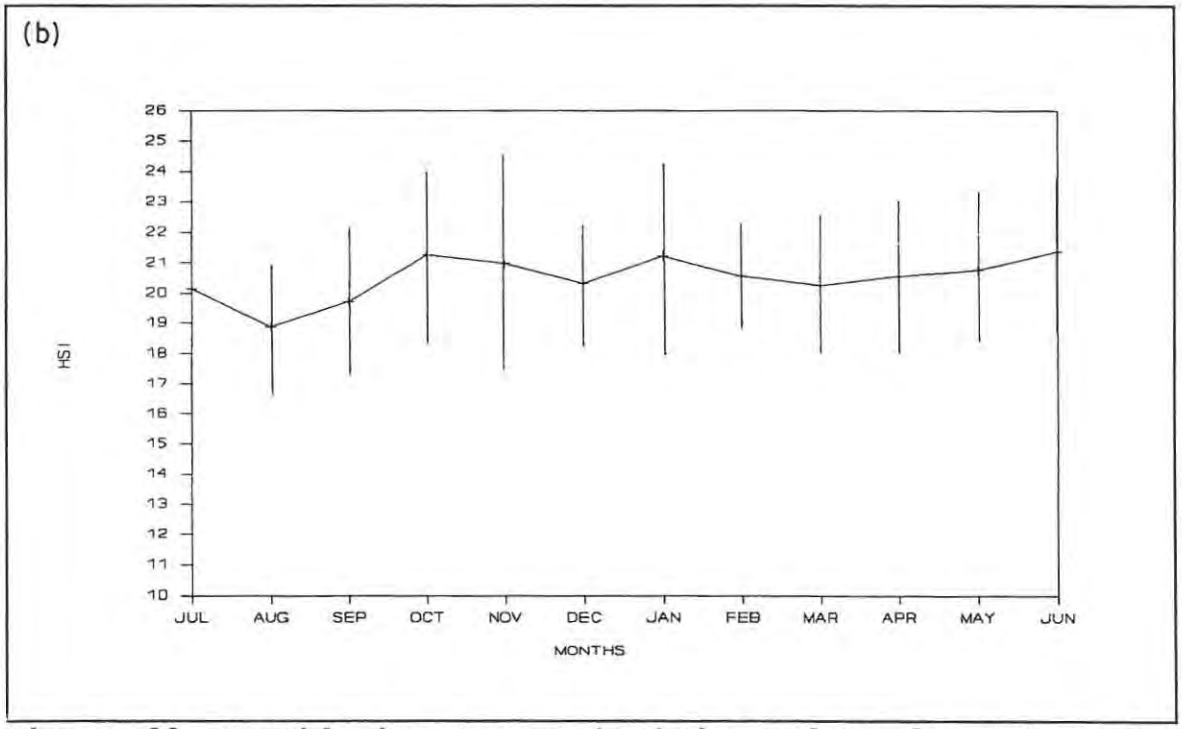


Figure 20. Monthly hepatosomatic index values for (a) marine and estuarine caught G. feliceps males and (b) females. Vertical bars represent 1 SD.

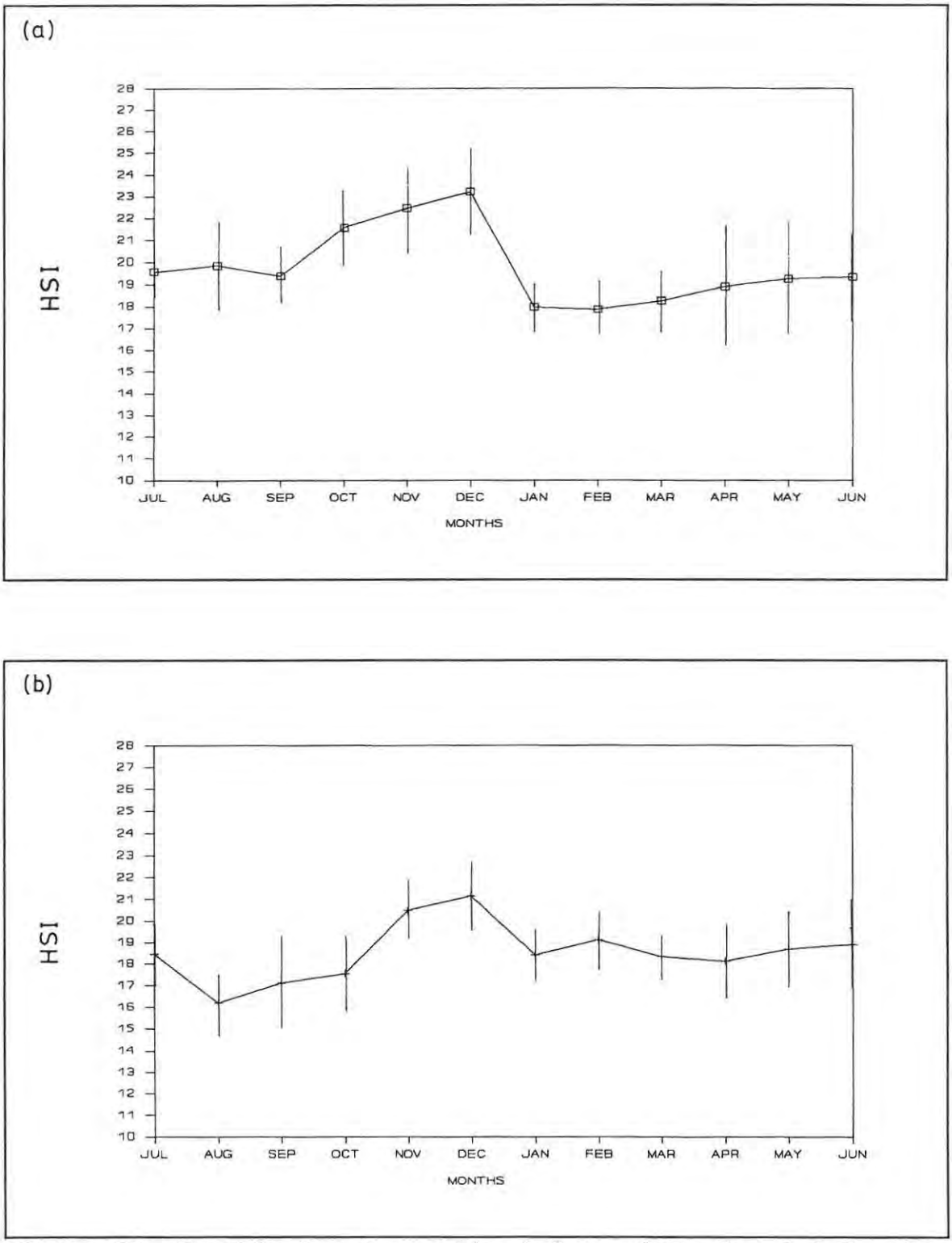


Figure 21. Monthly hepatosomatic index values for (a) G. ater males (mouth-brooders not represented), and (b) females. Vertical bars represent 1 SD.

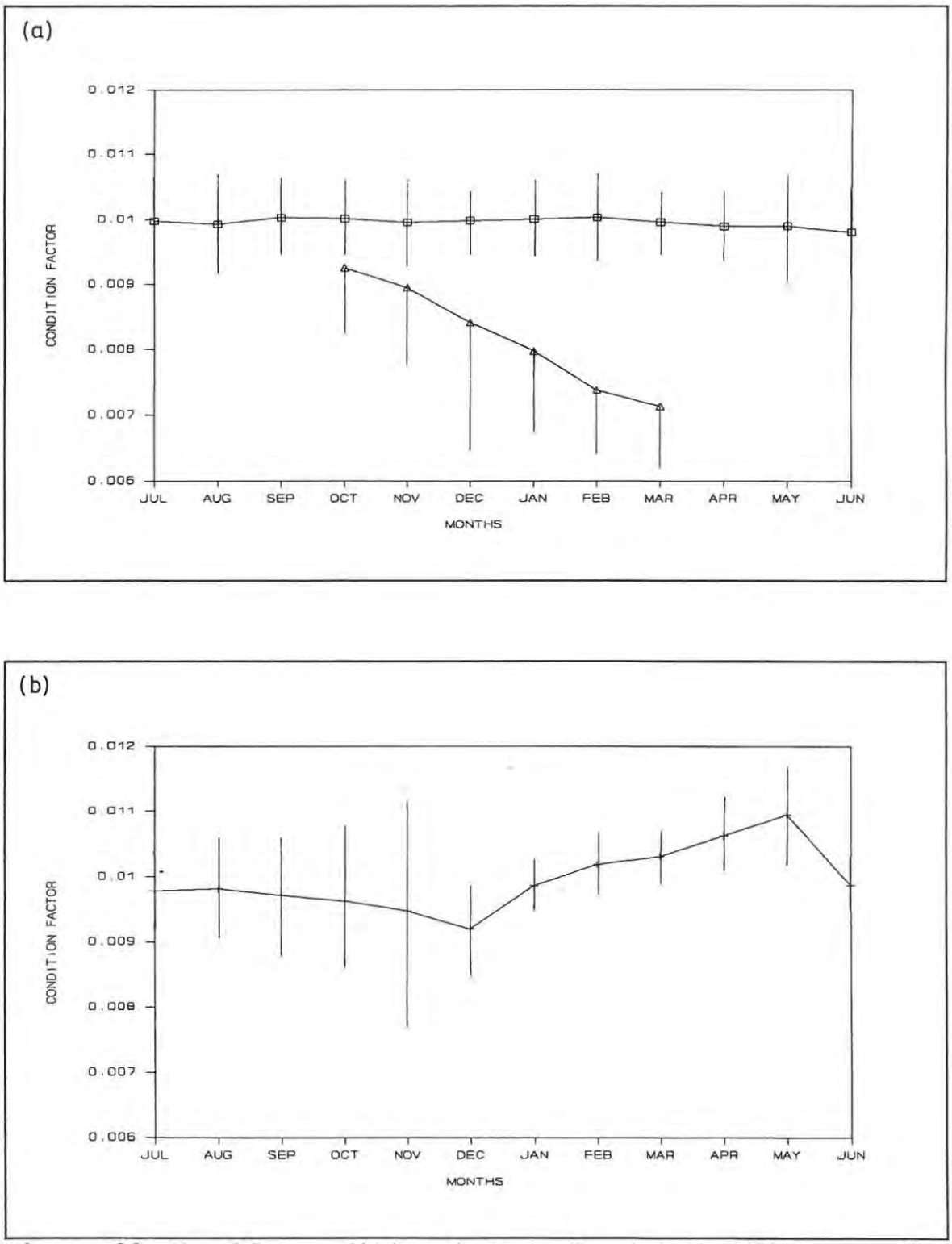
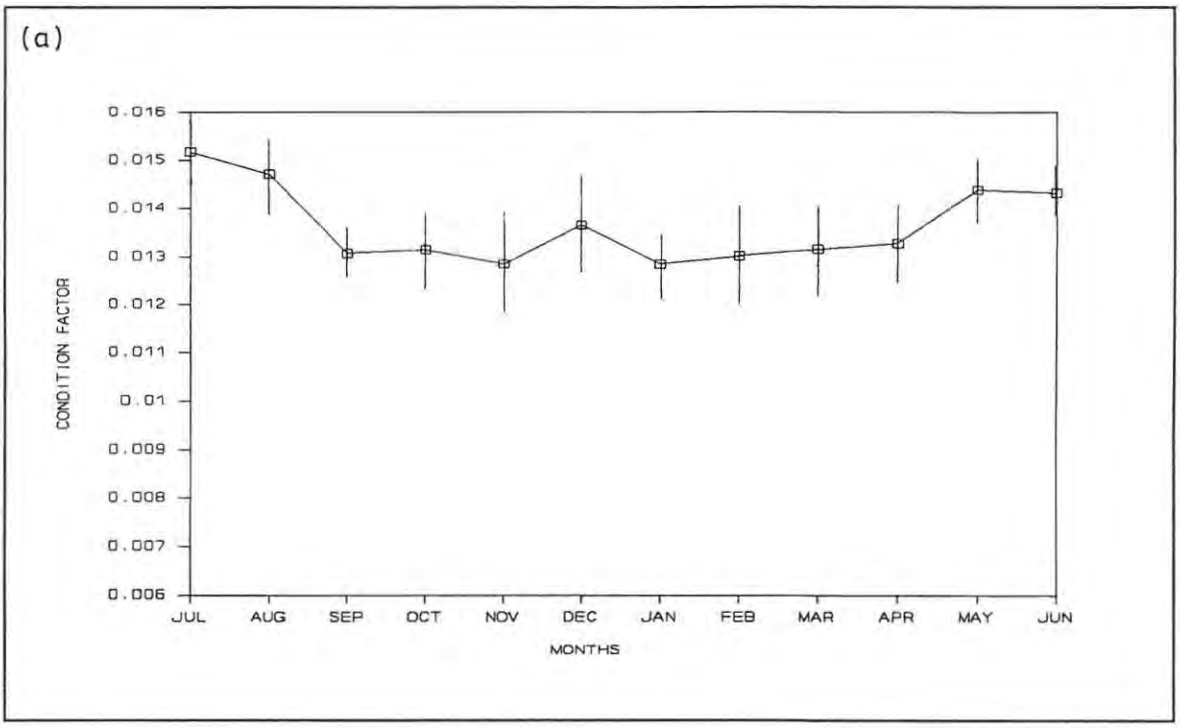


Figure 22. Monthly condition factors for (a) G. feliceps males (mouth-brooders plotted separately, standard deviations plotted below the curve for clarity), and (b) females. Vertical bars represent 1 SD.



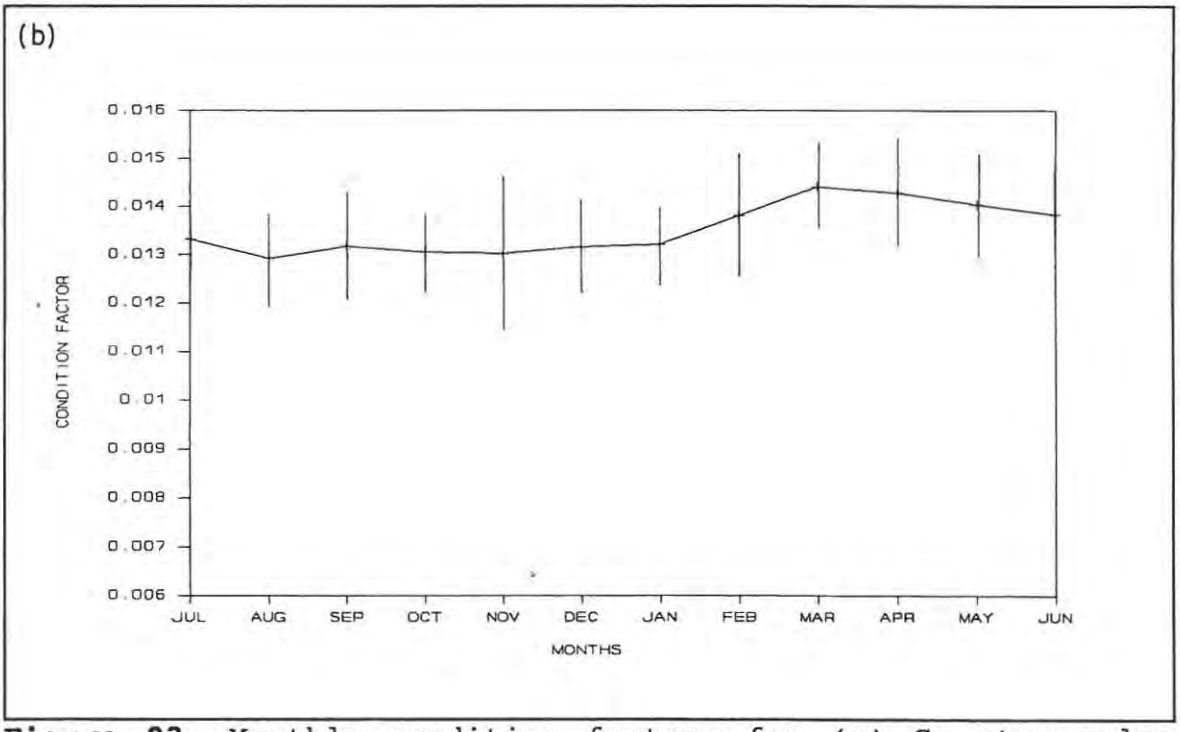


Figure 23. Monthly condition factors for (a) G. ater males (mouth-brooders not represented), and (b) females. Vertical bars represent 1 SD.

Relationship between fecundity and body dimensions

The influence of fish size and mass on the number and size of eggs is reflected in the regression analyses in Table V.

Table V. Regression equations for the relationships between fecundity and fork length, body mass and egg size for G. feliceps and G. ater.

	FL vs. Egg no.		Body wt. vs. Egg no.		Body wt. vs. Gonad wt.		Egg diameter vs. Egg no.	
	G. feliceps	G. ater	G. feliceps	G. ater	G. feliceps	G. ater	G. feliceps	G. ater
Constant	21.8104	33.4452	41.9646	42.5726	-13.8787	-1.7656	73.3454	52.7478
s.e. *y*	12.5538	8.7817	12.3805	8.7085	26.4583	14.3878	10.7913	5.6282
x coefficient	0.1022	0.0082	0.0256	-0.0163	0.0953	0.0607	-1.9821	-1.9369
s.e. *x*	0.0520	0.0488	0.0104	0.0118	0.0222	0.0214	0.2613	0.1535
r^2	0.03	0.02	0.04	0.02	0.11	0.07	0.28	0.58

Considering the r^2 values it could be concluded that there was no increase in fecundity with increasing fish size or mass. There was also no relationship between fish mass and gonad mass. The negative slopes (x-coefficients) of the relationships between egg diameter and egg number for the two species indicated that as eggs increased in size (matured), their numbers decreased (Figs 24 & 25). This meant that not all of the eggs originally present in, for example stage 3 ovaries, actually reached full maturation. This indicated that some developing eggs are resorbed during gonadal maturation. This was corroborated by the significant difference found between the mean number of eggs in stage 3 and stage 5 gonads in G. feliceps and in G. ater (Table VI).

Table VI. Test for significant differences between the number of developing eggs in stage 3 and stage 5 gonads for G. feliceps and G. ater.

	STAGE 3 OVARIES			STAGE 5 OVARIES					
	n	Mean Egg no.	sd	n	Mean Egg no.	sd	df	t-test (95% level)	sig dif
G. feliceps	43	57.90	9.72	66	49.27	12.79	107	2.0007	YES
G. ater	22	39.77	6.64	38	31.54	4.60	58	2.7331	YES

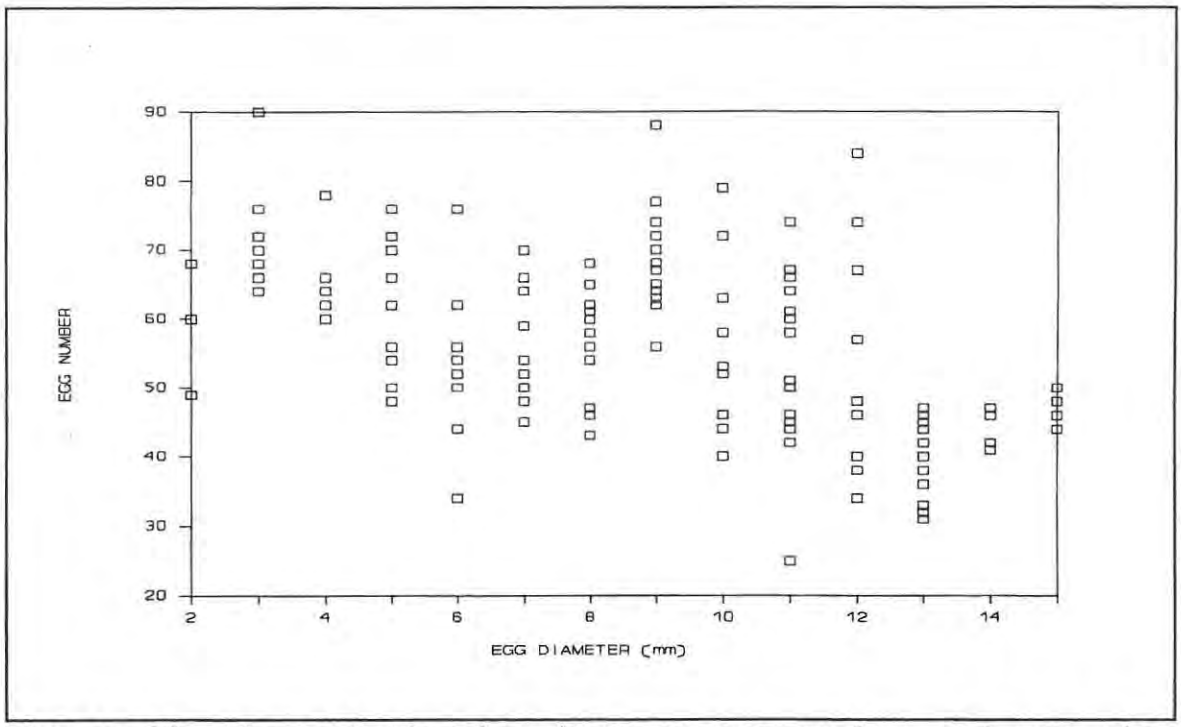


Figure 24. The relationship between egg number and egg size (i.e. gonadal maturation) in G. feliceps.

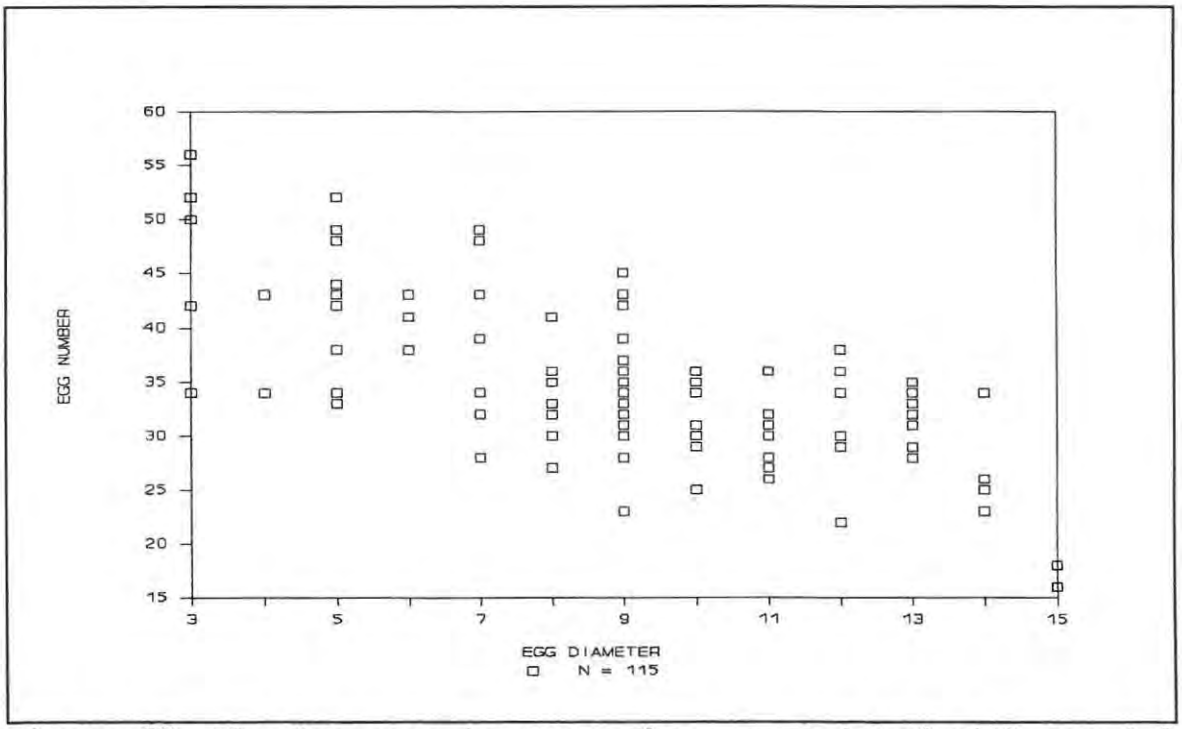


Figure 25. The decrease in egg numbers associated with gonadal maturation in G. ater.

A comparison of the average sizes and numbers of ripe eggs and of the relative fecundities in G. feliceps and G. ater gonads is presented in Table VII.

Table VII. Test for significant differences in egg size, egg number and relative fecundity (RF), between G. feliceps and G. ater.

	G. FELICEPS			G. ATER					
	Mean	sd	n	Mean	sd	n	df	t-test (P>0.05)	sig dif
Egg size	12.36	4.85	72	12.55	5.9	46	116	0.0936	NO
Egg No.	49.27	12.79	66	31.54	4.60	34	58	2.7331	YES
RF	0.119	0.037	82	0.099	0.024	39	119	1.6159	NO

The non-viable hyaline eggs were not included in the fecundity analyses for obvious reasons. However, they did constitute a substantial proportion of the mass of the gonads (± 22%), and the possibility that they played a role in reproduction could not be ignored. The mean number of hyaline eggs determined for three G. feliceps ovaries was found to be 23 013 (± 8 436). Assuming similar egg numbers for both ovaries, the total number of hyaline eggs per female was in the vicinity of 46 000.

The buccal volume of mouth-brooding males was found to be slightly larger than the volume of an average egg compliment from a single female (Table VIII). Although the mean number of embryos found in the mouths of brooding males ($x = 53$), exceeded the mean number of eggs from individual females ($x = 49$), this difference was not significant at the 95% level (t-statistic = -0.678, df = 90). This indicated that males probably incubated all of the eggs from one female, and that

the buccal cavity was large enough to accommodate the increase in embryo size following hatching.

Table VIII. Parameters used in the determination of brood volume in G. feliceps. Mean buccal volume for males is also presented.

	no. eggs per female	egg vol. (ml)	no. embryos brooded	calculated brood vol.	calculated buccal vol. (ml)
Mean	49.27	1.02	53.33	50.26	64.38
sd	12.79	0.18	8.43		8.63
n	77	256	15		13

Reproductive energy investment

In females, monthly hepatosomatic indices and condition factors revealed that liver and body weights remained relatively constant throughout the year, and they were not considered to be sources of reproductive energy. While the fat-somatic indices indicated that fat was accumulated during summer and autumn, it appeared to be utilised for gonadal maturation during winter. The energy contained in ripe ovaries would therefore be representative of the entire reproductive energy investment in females.

There were no significant differences between mean body mass (t-test = 0.7019; df = 89; $P > 0.05$) or liver mass (t-test = -0.3269; df = 89; $P > 0.05$) between similar sized males and females, suggesting that males did not accumulate body protein or liver reserves prior to mouth-brooding. There was, however, a significant difference in mean abdominal fat weight between the sexes at the time of spawning (t-test = 4.8015; df = 89; $P < 0.05$), indicating that males actively accumulated fat reserves prior to the mouth-brooding period.

In males, there was a significant difference in mean fat weight (t-test = 5.291; df = 80; $P < 0.05$), liver weight (t-test = 6.6199; df = 80; $P < 0.05$) and body weight (t-test = 4.8887; df = 80; $P < 0.05$) before and after mouth-brooding. By implication, therefore, these were all sources of energy which were utilised during the mouth-brooding period. These, together with the energy contained in ripe testes, were considered to be representitive of the total reproductive energy investment in males.

The energy and moisture content of the gonads, fat, liver and flesh of sexually mature G. feliceps between 315mm and 375mm (FL), are presented in Table IX.

Table IX. Energy (Kj/g) and moisture (percentage by weight) contained in the gonads, fat, liver and flesh of G. feliceps.

Sample	Sample no.	% Moisture content Mean	sd	Dry weight energy (Kj/g) Mean	sd	Wet weight energy (Kj/g) Mean
RIPE EGG	7	52.953	2.717	27.866	1.650	13.11
HYALINE EGG	7	93.048	2.245	19.294	1.123	1.341
TESTES	12	76.016	5.225	27.453	2.125	6.584
FAT	13	16.468	4.546	36.077	0.926	30.136
LIVER	9	75.091	2.416	25.817	2.212	6.431
FLESH	3	79.930	1.020	23.655	0.978	4.748

The amount of energy utilised during mouth-brooding was determined by converting the post-mouth-brooding losses in body, fat and liver weights into units of energy, using the data from Table IX. This energy, together with the energy contained in the testes, was considered to be representative of the reproductive energy investment by males.

The proportional body tissue (flesh), liver and fat energy inputs into mouth-brooding were 74.72%, 3.99%, 19.78% respectively. Males lost approximately 23.83% of their body mass, 50.74% of their liver mass and 76.4% of their accumulated fat reserves during mouth-brooding.

The weight ratio of ripe eggs : hyaline eggs : spent ovary was found to be 63.303% : 21.757% : 14.941% (n = 11). This enabled the separate extrapolation of the yolky and hyaline energy components from total gonad weights. The energy contained in the yolky eggs amounted to 98.91%, while the hyaline eggs contained the remaining 1.09%.

Reproductive energy investment by the sexes is presented in Table X. These data revealed that females invested approximately 35% less energy into reproduction than the males.

Table X. Reproductive energy investment in male and female G. feliceps.

	Pre-spawning mass		Post-mouth-brooding mass		Weight loss	Reproductive
	Mean	sd	Mean	sd	(g)	Energy (KJ)
Males						
BODY MASS	585.63	72.49	446.05	53.63	139.58	662.676
FAT MASS	7.17	5.35	1.35	1.91	5.82	175.392
LIVER MASS	10.84	2.27	5.34	1.40	5.50	35.371
GONAD MASS	2.67	1.74	0.63	0.11	2.04	13.431
TOTAL						886.870
Females						
YOLKY EGG MASS	43.72	6.14	0	0	43.72	573.169
HYALINE EGG MASS	15.03	2.57	0	0	15.03	20.155
TOTAL						593.324

Speculations on spawning behaviour

While courtship and spawning behaviour were not observed, a certain amount could be deduced from the reproductive data presented above and from the secondary sex characters. The following spawning scenario is envisaged: Males and females exchange recognition signals, possibly of an acoustic nature,

before pairing off. The female releases all of her eggs at once into the expanded pelvic fin cup. The eggs are adhesive and the egg mass is held between the pelvic fins while the male orientates himself appropriately and releases sperm. He then turns and takes the entire egg mass into his mouth. The sexes separate and the male seeks out a sheltered, protected environment in which to mouth-brood.

The observation that 12% of the G. feliceps males and 16% of the G. ater males with ripe gonads, lacked abdominal fat reserves, led to the speculation that sneaking might be employed as an alternative reproductive strategy in the two species. This behaviour was however not confirmed.

Discussion

Although there was a considerable overlap in the spawning seasons of the two species, peak spawning commenced one month earlier in G. ater than it did in G. feliceps. This phenomenon was observed during four successive spawning seasons and appeared to be consistent. While it is known that the onset of seasonal gonadal maturation in fish is controlled endogenously under the influence of exogenous environmental factors (Bye 1984), the reason for the temporal difference in spawning between these two closely related sympatric species is unclear. The timing of gamete release after completion of gonad ripening may be triggered by an environmental stimulus such as food availability, or potential food availability for the young in accordance with Cushing's (1975) 'Match/Mismatch' hypothesis, although this theory has recently been challenged (Sinclair 1988). It is more probable that the temporal separation in spawning time evolved prior to, or during the speciation process. If G. ater originated in a more northerly latitude than G. feliceps, it may have been geared to spawn slightly earlier in the year. The specific mate recognition system (Paterson 1978) would also have evolved prior to, or

during the speciation process, which presumably occurred in allopatry, and would have resulted in the maintenance of species integrity during their subsequent sympatry. Out of curiosity, an attempt was made at hybridising gametes from G. feliceps males and G. ater females in the laboratory. The experiment was unsuccessful and the zygotes ceased development after the 8-cell stage.

The cycle of accumulation and metabolism of visceral fat reserves occurred in response to different demands in the sexes. In females the fat reserves reached a peak in May and a low point in October-November, indicating that they were probably utilized for ovarian maturation, a common occurrence in fishes (e.g. Nikolsky 1963; MacKinnon 1972; Shul'man 1974 in De Vlaming et al. 1978; Delahunty & De Vlaming 1980; Pierce et al. 1980; Fishelson et al. 1985; Flath & Diana 1985). In males the fat reserves were accumulated during autumn and winter when gonad development was also occurring, and reached a peak in spring. Fat reserves declined rapidly after spawning, reaching a low at the culmination of the mouth-brooding phase, indicating that they contributed toward metabolic energy demands during this period. Guillemot et al. (1985) reported a similar phenomenon in several scorpaenid species in which accumulation of fat reserves occurred simultaneously with gonadal recrudescence, and served as energy for maintenance-metabolism during the post-spawning period when food was scarce. It appears that the female scorpaenids, which were from a live-bearing genus, and male ariids both accumulated fat reserves at the expense of increased growth in order to ensure their subsequent survival during the period of incubation.

The hepatosomatic index for the females of both species reached a low point in August (Figs. 20b & 21b), indicating that liver reserves may also have been involved in gonadal maturation. Liver reserves were also utilised quite considerably by males during the oral incubation period. The hepatosomatic indices for G. feliceps males (Fig. 20a) show that liver weight

decreased rapidly after the onset of mouth-brooding, indicating early mobilisation of the liver lipid store. Hepatosomatic indices also suggested that non-spawning males tended to begin resorbing liver energy approximately one month after the peak spawning period. In non-brooding G. ater males the liver weight continued to increase during the summer months (Fig. 21b). The graph shows a sharp drop-off after December when the post-mouth-brooding individuals re-entered the samples after re-commencement of feeding. The liver mass as a proportion of body mass in both species was low (approximately 1.9%), indicating that it is probably not an important energy storage organ.

The finding that the bulk of the mouth-brooding energy requirements in G. feliceps were derived from body musculature (74.7%), suggested that the muscle lipid content for this species was probably high. This was confirmed by Marais & Venter (1987), who found that lipid levels varied between 3.9% (in juvenile males) and 7.4% (in mouth-brooders incubating young embryos), in G. feliceps body musculature. Shchepkin (1971a,b), exhibited two different methods of energy storage in horse mackerel and scorpionfish respectively. Using biochemical analyses of liver and muscle lipid content he demonstrated that the former had a small proportional liver weight (1.5% of body mass) and a low liver lipid content (12%), compared to the latter (7% and 25% respectively). However, the muscle lipid content in horse mackerel (3%) was higher than that of scorpionfish (1.2%-2.7%). G. feliceps and horse mackerel therefore exhibit similar energy storage mechanisms.

Fat and protein are thus the two main forms of energy utilised during mouth-brooding in G. feliceps. Protein accumulation involves a number of processes including digestion, assimilation, catabolism and anabolism, and metabolically speaking, is an expensive energy source. Fat accumulation may be achieved directly through pinocytosis (Iles 1984), or through digestion and absorption (Phillips 1969). It is metabolically inactive and is deposited almost unchanged.

Fat would therefore be an energetically more economical energy source to accumulate, and males might be expected to utilise fat rather than protein as an energy source during mouth-brooding. It is clear from the results above that while fat is accumulated prior to mouth-brooding, the reserves are insufficient to meet the demands of the buccal incubation period and large amounts of protein are also metabolised.

Judging from the reproductive energy dynamics of G. feliceps it would seem improbable that an individual could manage to mouth-brood successfully without the stored fat reserves. Males lost an average of 24% of their body weight during mouth-brooding and without their high energy fat reserves (30.14 Kj/g), a proportionately greater amount of low energy body protein (4.75 Kj/g), would be needed to yield the same amount of energy. In the absence of fat reserves it is estimated that the total body weight loss would increase to approximately 34%.

The duration of mouth-brooding in G. feliceps is approximately 140 days (see Chapter 4). Males do not feed while incubating and the significance of feeding cessation is highlighted by the work of Iles (1984), who found that the maintenance of an active epithelium in the alimentary canal was the largest non-reproductive source of protein loss in herring.

The long period of starvation during mouth-brooding in G. feliceps leaves the males considerably emaciated at the end of it, and the monthly condition factors for G. feliceps mouth-brooders (Fig. 22a) clearly demonstrate the marked seasonal drop-off in condition. From the above information it is clear why it is the males and not the females that perform the parental care role. Energetically speaking it is unlikely that females would be able to produce the full compliment of eggs, mouth-brood them to term and also recover in time for the next spawning season.

If it is true that males are not able to mouth-brood unless they have accumulated abdominal fat reserves, the observation that 12% of G. feliceps and 16% of G. ater males with fully mature testes did not have any fat, would imply that they intended to spawn without assuming the burden of mouth-brooding. This suggests that these males may employ sneaking as an alternative reproductive strategy. Sneaking is fairly common in fish (e.g. Gross 1984; Chan 1987; Noakes et al. 1989), and also occurs in other animal groups (e.g. isopods, Shuster 1989 and grasshoppers, Alexander & van Staaden 1989). The implications of possible sneaking behaviour in ariid reproduction will be discussed at greater length in the General Discussion (Chapter 7).

The plots of fork length against accumulative percentage sexual maturity indicated that mature G. feliceps spawned each year (Fig. 14). However, approximately 10% of the mature G. ater male population failed to do so (Fig. 15a). Closer examination of the data revealed that where G. ater individuals of mature size exhibited undeveloped testes during the spawning season, they had also not accumulated any fat reserves. Whether the lack of fat was a cause, or a symptom, of spawning failure or whether it was unrelated to the latter is not known. It is conceivable that if the duration of mouth-brooding in G. ater was even longer than that found for G. feliceps, some of the males might not have been able to recover condition in time for the successive spawning season. A certain proportion of G. ater males may therefore only spawn every alternate year.

In G. feliceps a small percentage of males which had both fat reserves and ripe gonads also failed to spawn. These individuals may simply have been unable to find a mate. Females in the process of resorbing ripe eggs were also encountered in the samples toward the end of the spawning season, indicating that this phenomenon was common to both sexes. This finding would tend to corroborate the spawning behaviour scenario

described earlier in which it was envisaged that males and females spawned in pairs, as opposed to groups.

G. feliceps was thought to be monogamous since the number of eggs produced by females was not significantly different from the number of embryos in the average male brood. In addition, all of the embryos being brooded by individual males were always at the same stage of development. Dmitrenko (1970), using a volumetric comparison of egg-batch and male buccal cavity, also deduced that males carried the eggs from a single female in Arius thalassinus from the Arabian Sea. However, he found that females of the species produced up to three batches of eggs during one spawning season. This is the only account in the literature of serial spawning in an ariid, and if this mode of spawning does in fact occur, it would probably be manifest in a sex ratio which heavily favoured males. This is because each male would most likely only be capable of brooding one batch of eggs each year, as indicated by the results from this study. Dmitrenko (op cit.) does not present sex ratio information, although Bawazeer (1987) demonstrated that the sex ratio for A. thalassinus in Kuwaiti waters differed significantly from unity in all size classes, but that neither sex was consistently favoured.

The literature presents conflicting results with respect to ariid fecundity vs. body size relationships. Some species exhibit positive correlations (Etchevers 1978; Mishima & Tanji 1985; Rimmer 1985a; Reis 1986a; Coates 1988), while others reveal no correlation (Tobor 1969; Mishima & Tanji 1985). The results of this investigation supports the latter (Table V). Since 50% sexual maturity occurred at 295mm, and the maximum recorded size for G. feliceps females in the study was 375mm, approximately 80% of their growth was completed before attainment of sexual maturity. A closer examination of the literature revealed that for species in which there was no correlation between body length and fecundity, between 78% and 80% (n = 3) of their growth was completed prior to sexual

maturity. For species in which there were positive fecundity - body size relationships, sexual maturity was reached earlier, when between 40% and 77% (n = 7) of their growth had been completed.

Few authors have discussed the function of the hyaline eggs in ariids and only two suggestions have been put forward in the literature. Firstly, that they serve as nourishment for the male prior to commencement of mouth-brooding (Gunter 1947). Secondly, that they effect a lowering of the specific gravity of the egg mass and prevent it from sinking into the 'ooze' of the substratum (Dmitrenko 1970).

Menon (1984) found hyaline eggs in the buccal cavities of four mouth-brooding ariid species from Indian waters. In all cases, sampling must have occurred soon after spawning as in each instance the eggs were still adhesive, a property which is lost after a few hours (see Chapter 4). Menon (op cit.) observed two distinct sizes of hyaline eggs (0.25mm-0.8mm and 1.9mm-3.3mm), along with the ripe yolky eggs in the mouths of adult males. Dmitrenko (1970) encountered partly digested 'yolkless' hyaline eggs in the stomachs of two mouth-brooding male A. thálassinus, indicating that these eggs were indeed ingested. However, in the present study it was found that the hyaline eggs were of little nutritive value (Table IX), and also that they were negatively buoyant. Therefore neither of the above suggestions regarding their function seems convincing. While no concrete suggestions could be made on the strength of this study, the following ideas came to mind:

a) Hyaline eggs may be the source of a chemical stimulus inhibiting feeding in males, although yolky eggs could serve this function equally well,

b) as the hyaline eggs are released ahead of the yolky eggs at spawning they may serve as egg dummies to stimulate males to commence fertilization,

c) the hyaline eggs may be a remnant from a more fecund ancestral condition, and may be representative of an

evolutionarily incomplete process of change to a less fecund animal. Siluroids are thought to have evolved in fresh water (Greenwood et al. 1966), and the vast majority of present day fresh water siluroids are highly fecund. Since all of the marine representatives (Ariidae, Aspredinidae & Plotosidae) are either mouth-brooders or guarders with low fecundities, it seems that there may have been a shift toward lower fecundities in these families.

Biochemical analysis of the constituents of hyaline eggs and a microscopic examination of their cellular structure might contribute toward our understanding of their role in reproduction. Gibaeva & Ermolina (1972 in Rimmer & Merrick 1983), detailed differences in the cell structure of the follicular epithelium in hyaline and yolky oocytes during the later stages of oogenesis in Arius felis, although no explanation as to the functional significance of the finding was presented.

The reasons for the secondary sex characters observed in G. feliceps and G. ater are also open to speculation. Rimmer (1985a) found that the epithelium of the palatine tooth patches in Arius graeffei thickened and grew over the teeth during incubation thereby protecting the young from damage. The mucus coating on the pharyngeal and palatine tooth patches in G. feliceps and G. ater could serve a similar function. The need for such protection was highlighted by the frequent coughing motions exhibited by adults during mouth-brooding, which lead to considerable movement of the embryos within the buccal cavity (pers. obs.). The embryos were separated from the teeth on the pre-maxilla and dentary by an oral valve, and the latter were not mucus-coated.

Sexual dimorphism in the pelvic fins has been described in several ariids (Lee 1937; Dmitrenko 1970; Rimmer 1985b). The pelvic fins of females were larger than those of the males in all instances. In some species, fleshy hook-like structures

appeared on the adaxial (dorsal) surfaces of female pelvic fins during the spawning season. These protuberances had the effect of orientating the pelvic fins in a vertical plane and formed a trough on either side of the vent. Some authors speculated that the female clasped the male in her enlarged pelvic fins during spawning, while others suggested that the fins were modified to hold the eggs while the male fertilized them. While the method of egg transfer between female and male has not yet been observed in ariids, it is most probable that the enlarged pelvic fins in females serve to hold the adhesive egg mass at spawning until the male has fertilized them and is able to turn around and take them up into his mouth. It seems unlikely that the pelvic fin modification would have evolved if the females laid their eggs directly onto the substratum as suggested by Gerard (1958 in Dmitrenko 1970).

Sexual dimorphism in the cleithra of ariids has not been previously reported in the literature. In G. feliceps and G. ater it is probably associated with sex-specific sound production or reception. Rapid backward and forward movement of the pectoral spines sets up a stridulation between the pectoral spine condyles and their sockets. Viewed laterally, the trajectory of the pectoral spine tip during repeated anterior-posterior motions, is elliptical. On the posterior stroke the tip of the spine is lowered slightly in a ventral direction, while on the anterior stroke it is elevated slightly. Sound is produced during the posterior stroke, when the many fine, transversely orientated ridges on the ventral surface of the superior condyle come into contact with the rugose, juxtaposing surface of the pectoral groove within the socket (terminology after Halstead 1978). The left and right pectoral spines are moved backwards and forwards alternately, resulting in the production of continuous sound. Sound was occasionally produced by the animals when they were handled, and the considerable vibration in the vicinity of the cleithra which accompanied it, could be clearly felt in the fingers. The post-humeral process of the cleithrum forms a close association

with the air bladder in that the medial surface of the former abuts directly onto the lateral surface of the latter. The air bladder in ariids is associated with both sound reception and sound amplification (Tavolga 1962, 1971), and it is envisaged that the sexual dimorphism of the cleithrum may play a role in one or both of the above. The difference in shape might modify the acuity of sound perception or the tone of the sound produced in the sexes, implying that sound communication may play an important role in courtship.

The fatty deposit that appears on the female pectoral spines of G. ater during the spawning season might also be associated with sound communication. The fat deposit would increase the density of the spine, which in turn would alter the pitch of the sound produced during stridulation. As G. feliceps females do not develop this fatty deposit it is conceivable that this phenomenon in G. ater may serve as an effective specific mate recognition system (sensu Paterson 1978) for reproduction in dark or highly turbid environments.

In conclusion, it is evident that G. feliceps and G. ater have very similar reproductive strategies. While G. ater has a significantly lower fecundity, the relative fecundities of the two species are the same. Fecundity does not increase as a function of body size. Reproduction in both species is energetically more expensive for the male and it is possible that a small percentage of males may adopt sneaking as an alternative reproductive strategy. Energy requirements for maintenance metabolism during mouth-brooding are derived chiefly from body musculature and coelomic fat reserves, while a small proportion comes from the liver. Pair spawning occurs and the males incubate the entire brood from a single female. Sound communication may play a role in reproduction.

CHAPTER 4 - EARLY ONTOGENY

Introduction

The paternal mouth-brooding habit of G. feliceps and G. ater leads to the reproductively active male population being excluded from the fishery for an undetermined period each year. Since fishing effort at Port Alfred is relatively constant throughout the year (Hecht & Tilney 1989), there is a danger that differential exploitation of the sexes might lead to an imbalance in the sex ratios. As both species are monogamous, skewed sex ratios would have a detrimental effect on their population dynamics. If skewed sex ratios should arise then, from a fisheries management perspective, knowledge of the buccal incubation period would be imperative for it to be rectified.

Buccal incubation periods for ariids in the literature vary between six and nine weeks (for review see Rimmer & Merrick 1983). Investigation of source material revealed, however, that these had not been reliably established and were no more than estimates (Gudger 1916; Lee 1937; Merriman 1940; Atz 1958; Tobor 1969; Rimmer 1985a). While the aforementioned authors described aspects of early development in ariids, none of them had monitored development for the duration of the mouth-brooding period. This study represents the first documented account of ariid ontogeny from activation through to release of young from the adult buccal cavity.

Since attempts to induce spawning in captive animals failed, the duration of the buccal incubation period had to be determined using captured mouth-brooding animals which were transferring to aquaria in the laboratory. As the age of the embryos being incubated by wild-caught mouth-brooders was unknown it was necessary to artificially spawn adult fish and

record the time for embryonic development through to the stages identified from wild-caught broods.

Ontogeny is a genetically determined hierarchical sequence of dynamic developmental steps, generally considered to start at activation and end at death. The rate and direction of differentiation and growth is also influenced by the extra-nuclear environment (Lovtrup 1974, 1984; Jantsch 1980; Hall 1983; Caro & Bateson 1986), so that developmental events are orchestrated through genetic, epigenetic and environmental interplay to produce an organism with maximum survival potential.

It has been suggested that ontogeny proceeds in a saltatory fashion (Balon 1981c, 1984, 1986, 1989). Central to this theory is the idea that early development proceeds as a sequence of steps during which development is gradual, separated by periods of accelerated change, termed saltations. While the theory was not central to this study it was taken into consideration in the interpretation of the observed sequences of events.

While the primary objective of the study was to determine the duration of the buccal incubation period, it was anticipated that a knowledge of the nature and timing of developmental events occurring during the early ontogeny of G. feliceps would allow parallels to be drawn with mouth-brooding species from other fish families.

The study concentrated on the early development of G. feliceps only. G. ater were excluded because of the difficulty of capturing mouth-brooding individuals in their sub-tidal reef habitat.

The holding system

The holding facility comprised a recirculating system in which water was gravity fed from a 1000 liter header tank, through an ultra-violet filter to the incubators and then into a 2m X 0.8m X 0.5m gravel filter. An electric pump, activated by a float-switch, moved the water from the filter back to the header tank. A 15 hour light : 9 hour dark photoperiod was maintained. The salinity within the system varied between 35ppt and 38ppt. Water temperature fluctuated according to ambient thermal changes and ranged between 20.0°C and 26.0°C, with a mean of 21.9°C. This was similar to the mean river temperature (21.0°C) for the same time period, although the temperature range in the river was greater, being between 15.5°C and 25.0°C.

The water flow rate through the incubators was held constant at approximately 25 litres per minute. Air stones were used to oxygenate the incoming water. Three different incubation chamber designs were used (Fig. 26). The funnel type was effective although at the desired flow rate the embryos began to tumble. Tumbling did not occur in the buccal cavity (pers. obs.), and it was considered inadvisable for the incubation of telolecithal eggs (E. Balon pers. comm.). This system was therefore abandoned. The second system comprised a series of mesh-bottomed trays stacked one on top of the other and held in a rectangular chamber in which water was introduced from above. Although this system functioned well, it was awkward in that access to the lower trays necessitated the removal of the upper trays. The third design comprised a 1.5m section of 150mm diameter PVC piping, blocked off at either end and with a series of large holes drilled along a horizontal plane allowing the insertion of plastic specimen bottles. A 25mm tube at either end acted as the inlet and outlet respectively. Sections of the sides and bottoms of the specimen bottles were cut away and replaced with fine mesh gauze, allowing water to pass

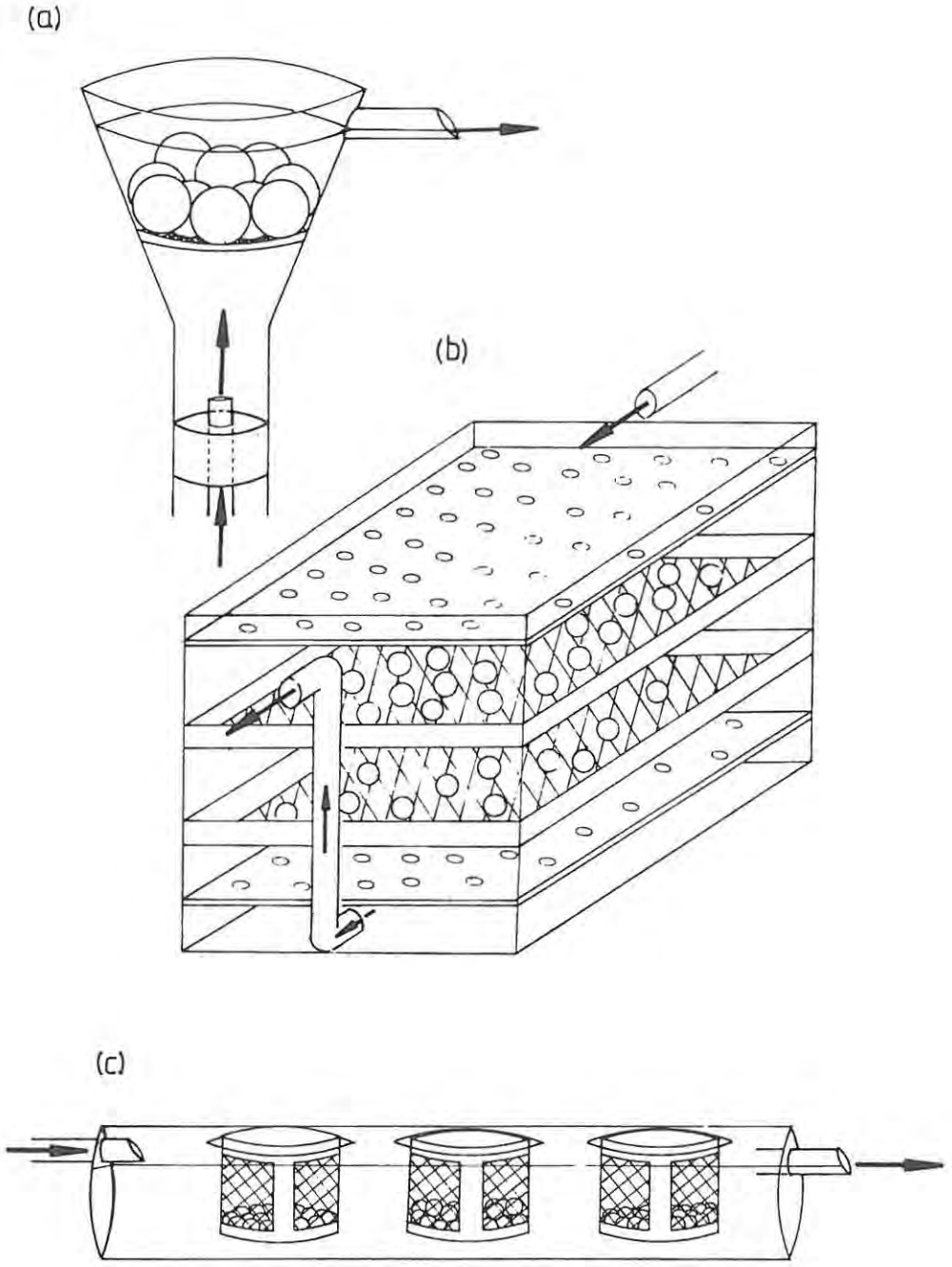


Figure 26. Incubation chamber designs. (a) Funnel type, (b) tray type and (c) bottle type. Arrows indicate water flow. (Not drawn to scale.)

through them. Different batches of embryos could be held independently in the incubator and all embryos were easily accessible. A problem encountered in all three incubator designs was that of invertebrate infestation, which proved to be a major stumbling block in the study. Sessile cilliates, copepods and turbellarians settled on, or burrowed into the eggs, causing high mortalities. Preventative measures including the use of fine mesh filters, ultra-violet water sterilisers and formalin and fresh water flushing proved largely ineffective.

Embryos were removed from captured mouth-brooding G. feliceps on a monthly basis over a period of approximately five months. Several broods at different stages of development were observed, enabling the generation of an overall picture of the early ontogeny. A consequence of this method, however, was that only approximate ages could be assigned to the various developmental steps.

The approximate duration of the entire oral incubation phase was determined by holding captured mouth-brooding fish in aquaria. Mouth-brooders were caught early on in the spawning season and in each instant two to three embryos were removed from the buccal cavity in order to establish the degree of embryonic development, and hence approximate age. Five mouth-brooders held in aquaria incubated their young to term.

In order to elucidate the timing and duration of the activation and cleavage phases which were seldom encountered in the broods of wild-caught fish, ripe male and female G. feliceps were caught off Port Alfred on hook and line and transported to the laboratory alive. Eggs were stripped and fertilised using macerated testes from sacrificed males. Sea water was added until the egg mass was submerged and then left undisturbed for a few minutes before individual eggs were pried apart by hand and transferred to the incubators. After three to four days the outer adhesive membrane began to flake off. At this time all

eggs were individually stripped of this layer by gentle rubbing between the finger and thumb. Considering the size of the eggs (mean = 12.4mm) this was an easy and effective method to use. They were kept underwater at all times and were not damaged during the cleaning process.

Embryos were submerged in a petri-dish and viewed under a Nikon binocular microscope using either transmitted or reflected light, the latter from a cold light source. The embryos were viewed vertically (i.e. from above) and illustrated with the aid of a camera-lucida attachment at variable magnification between 6.6X and 30X. In initial sketches coloured pencils were used as an aid for recording the direction of blood flow. Red was used to denote blood moving away from the heart, while blue was used to indicate vessels carrying blood toward the heart. Selected steps in development were photographed using AGFA XR 100 colour film and FUJI-CHROME 100 ASA colour slides.

Some embryos were excised from the egg envelope and orientated horizontally under the microscope to facilitate observation of ventrally situated structures. Tricaine methane sulfonate (MS-222) was used to anaesthetise excised embryos, inhibiting movement during photography and illustration.

Skeletal development was monitored using a clearing and staining technique. The methods of Taylor & Van Dyke (1985) and Balon & Flegler-Balon (1985), specifically designed for use with small fish, were followed.

Ventilation rates were monitored as follows: the number of inhalations per minute was recorded for non-brooding adult males, for mouth-brooders carrying unhatched embryos and for mouth-brooders carrying hatched embryos.

The terminology of Balon (1975) was used to describe the intervals of development. The different phases, cleavage (C), embryo (E) and free embryo (F) were divided into recognisable

steps, each of which were assigned a code (Balon 1981a). For example, $E^2 6$ would represent the second step in the embryonic phase and the sixth step since activation. Developmental steps were subjectively identified on the strength of marked ontogenetic events and did not necessarily conform to saltations in ontogenetic development. The timing of the ontogenetic events was initially recorded in days, hours and minutes. For example 0:12:30 represents 12 hours and 30 minutes. Development was initially monitored every four hours. After approximately 36 hours when the 64-cell stage was reached cleavage could no longer be accurately described, development was very slow and the frequency of observations was therefore reduced. Subsequent development was recorded on a daily basis. The skeletal nomenclature adopted was after Gregory (1959).

Results

The yolky and hyaline eggs became strongly adhesive on being spawned. Manual stripping of gravid females resulted in a plug of small hyaline eggs (diameter 0.69mm ± 0.15mm, n = 50) being released first, which were followed by the yolky oocytes. The latter were interspersed with hyaline eggs larger than those which formed the initial egg plug (diameter 1.75mm ± 0.19mm, n = 50). The mature eggs were slightly oval in shape and measured approximately 15.65mm (± 0.80mm, n = 50) X 13.19mm (± 0.44mm, n = 50) (Plate V).

Apically, the adhesive outer membrane was arranged into several bulges (usually between 5 and 6), which formed a stellate arrangement around the micropyle (Fig. 27). A depression in the vitelline membrane was visible immediately beneath the micropyle. At this stage the female pronucleus was randomly orientated relative to the micropyle. The yolky oocytes were bright yellow, which may be indicative of a high carotenoid respiratory pigment content (Balon 1977, 1979). The dense yolk was uniformly distributed and did not contain oil globules.

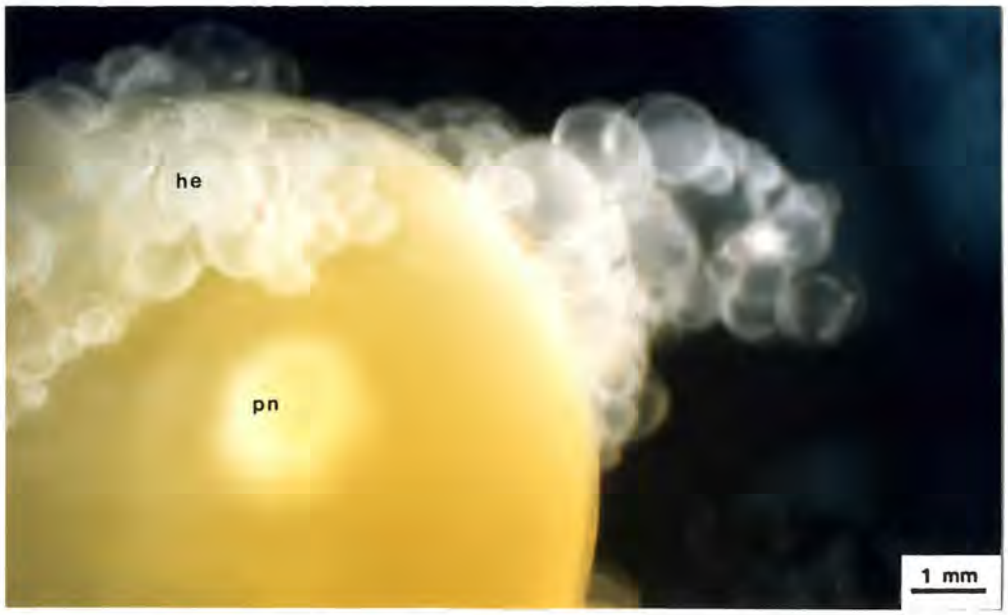


Plate V. Photograph demonstrating the nature of the hyaline eggs (he) and the pronucleus (pn). 6.6X Magnification.

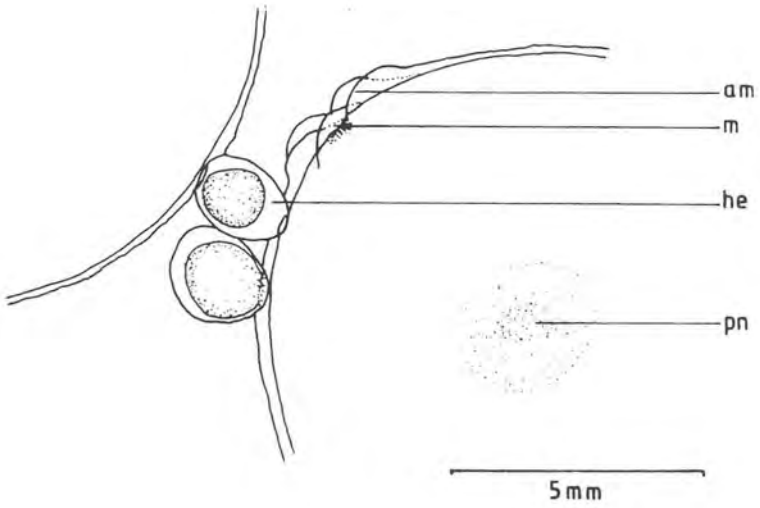


Figure 27. Detail of the mature egg before activation showing the stellate arrangement of folds in the adhesive membrane (am), forming the micropyle (m), pronucleus (pn), and the small, interstitial hyaline eggs (he), spawned along with the yolky eggs.

Electron micrographs revealed that the outer surface of the egg envelope was rugose in appearance, while the inner surface was

dominated by a dense arrangement of pores, each of which was approximately 0.6 µm in diameter. The egg envelope was approximately 24.8 µm thick (Plate VI).

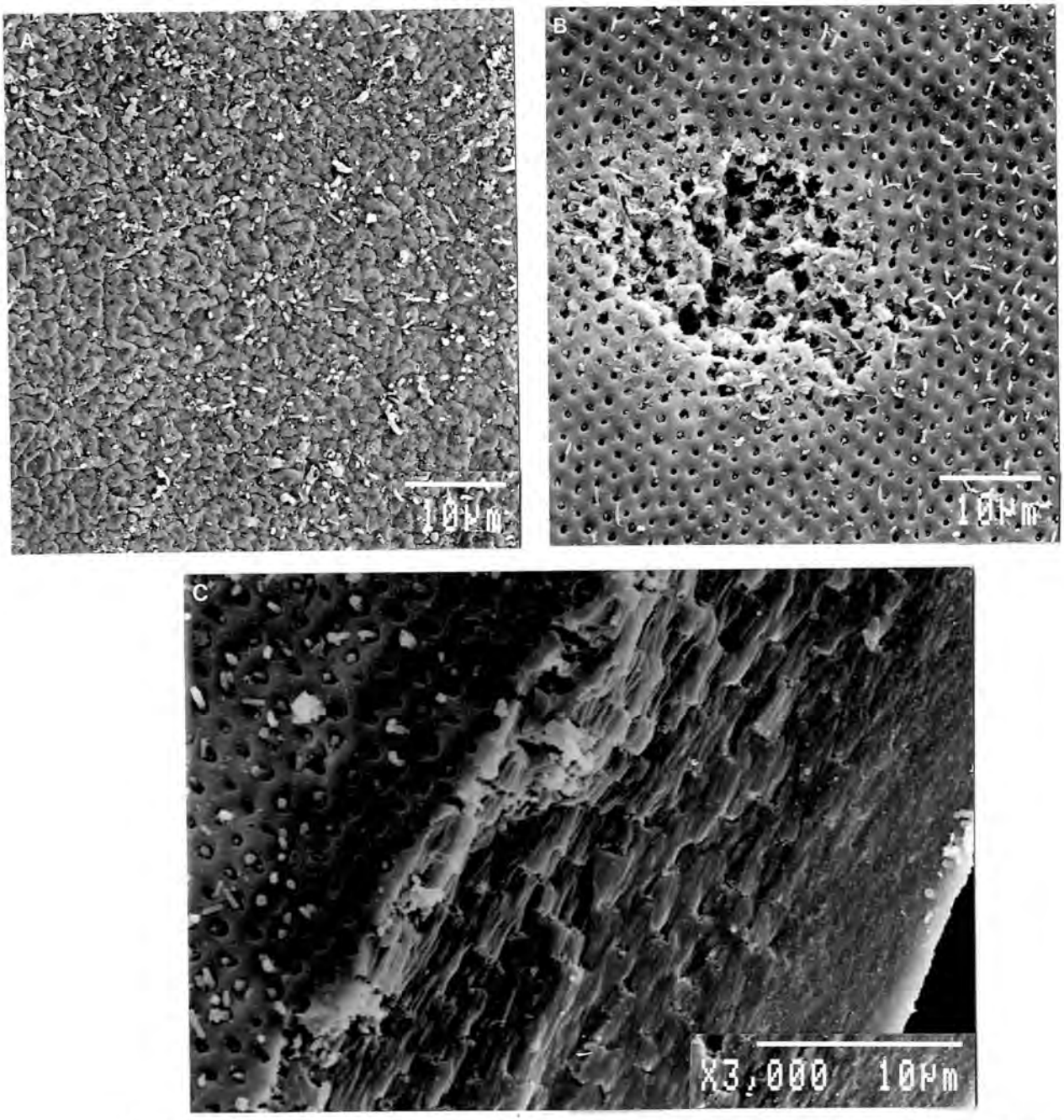


Plate VI. Electron micrographs of the egg envelope. a) Rugose outer surface, b) hatching enzyme damage to the pitted inner surface and c) cross section through the egg envelope.

After artificial fertilisation of eggs in the laboratory the longest period of embryonic development observed was 28 days, corresponding to approximately one fifth of the total mouth-brooding period (see later). The embryos died at this time due to cilliate, copepod and turbellarian infestation. These time-series data were crucial to the study as they provided a foundation for the subsequent ageing of wild-caught broods, which were used to describe ontogenetic development beyond the age of 28 days.

Descriptive early ontogeny of G. feliceps

(Note: C = cleavage phase, E = embryo phase, F = free-embryo phase.)

Cleavage phase

Step $C^1$1

Activation: Period 0:00:00 - 0:19:00:

After introduction of male gametes the egg hardened and a perivitelline space formed apically at one end of the egg at approximately 0:12:30. The yolk moved freely within the egg envelope and in all eggs the pronucleus was orientated directly beneath the micropyle. Cytoplasmic streaming was not observed.

Step $C^2$2

Cleavage: Period 0:19:00 - 2:22:00, after which the blastodisc constituted a ball of very small blastomeres (morula), raised above the yolk surface:

The first mitotic cell division occurred after 0:19:00. The second division occurred at right angles to the first, at 0:23:20. The third division was parallel to the first and occurred at approximately 1:03:30. Each successive division resulted in a decrease in the size of the blastomeres. After the 8-cell stage division was often asynchronous and cells were difficult to count. The 16, 32 and 64-cell stages occurred at approximately 1:05:00, 1:08:45 and 1:12:15. After 2:22:00,

the blastomeres were minute and arranged in a near-spherical ball-shaped morula. This morula was situated in a depression in the yolk (Fig. 28), which was now punctate and covered with small, freckle-like spots. The outer, previously adhesive membrane, began breaking down and sloughing off. The diameter of the blastodisc had remained constant at approximately 2.1mm.

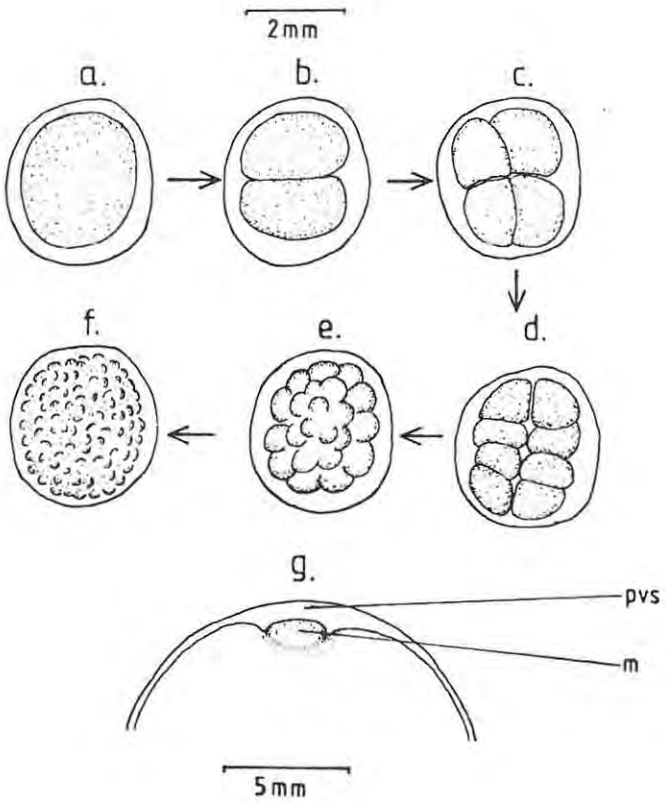


Figure 28. Cell division after fertilisation. a) Fertilised zygote, b) 2-cell (00:19:00), c) 4-cell (00:23:00), d) 8-cell (01:03:30), e) 32-cell (01:08:00), and f) morula (02:22:00) stages. g) Lateral view of morula (m), recessed into the yolk, and the peri-vitelline space (pvs).

Step $C^3 3$

Epiboly and embryogenesis: Period 3:00:00 - 10:00:00, after which the syncytium had commenced migration around the yolk-sac and the embryonic shield had become evident:

After approximately 04:00:00 to 04:20:00, the blastodisc had become flattened over the yolk. The germ ring was distinct as a zone of granular appearance around the blastodisc. Epiboly commenced after seven days when the syncytium began expanding over the yolk surface, within the boundary of the expanding germ ring (Fig. 29a). Embryogenesis commenced after nine days when the germ ring had advanced approximately one third of the way around the yolk mass. The embryonic shield became evident and lengthened as the syncytium advanced over the yolk, the presumptive caudal region remaining at the edge of the germ ring (Fig. 29b). There was no evidence of organic differentiation during this step.

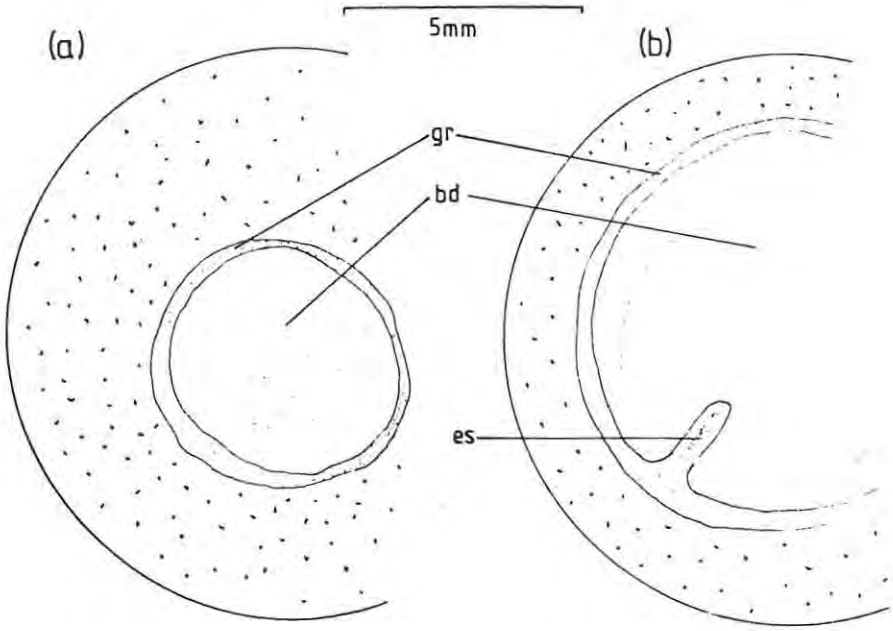


Figure 29. a) Flattened blastodisc (bd) surrounded by the germ ring (gr) (04:20:00), b) early embryogenesis (9 days) demonstrating the embryonic shield (es) and the expanding germ ring. The yolk surface is speckled.

Embryonic Phase

Step $E^{1}4$

Commencement of organogenesis: Period 10 - 23 days, after which the full compliment of somites was present, the tip of the tail was free and cephalic differentiation had commenced. A simple heart, a few rudimentary vitelline blood vessels and a tube-gut had appeared:

The presumptive notochord and the first somites appeared after approximately 10 days. At 14 days the germ ring covered half of the yolk and approximately 13 pairs of somites were visible. The presumptive notochord was well defined. By the 18th day the optic vesicles had differentiated, the otocysts were distinct and 25 pairs of somites were visible (Fig. 30). The pericardial cavity began to form beneath the embryo in the region between the optic vesicles and the otocysts, in a depression in the yolk. Differentiation of the brain into left and right halves occurred in the region anterior and adjacent to the otocysts.

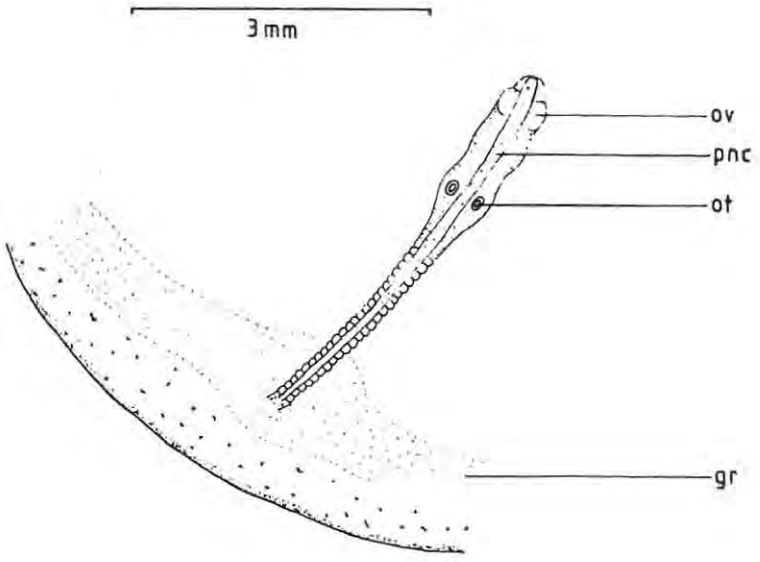


Figure 30. Beginning of cephalic differentiation at the 25-somite stage (18 days). Presumptive notochord (pnc), optic vesicles (ov) and otocysts (ot). Epiboly approximately one third complete.

By day 20, epiboly was two thirds complete and the tail was free from the yolk-sac and had lifted above it. The tail was short, thick and rounded. The full compliment of somites, approximately 45, were visible. The optic vesicles were well defined. The hind-brain area showed invagination and differentiation into left and right hemispheres. The otic capsules were distinct and oval in shape, although otoliths were not visible. The embryo was 5.4mm long. The head length (measured up to the first somite) was 1.9mm, and the postanal trunk length was 1.9mm.

Removal of the egg envelope and manipulation of the embryo at 22 days revealed a simple tube-like heart pulsing at 24 beats per minute, although no blood cells were visible. Olfactory placodes were present. The mid- and hind-brain demonstrated considerable invagination. Three pairs of rudimentary gill pouches protruded ventro-laterally immediately posterior to the otic capsules. Two pairs of otoliths were visible in the otic vesicles. Epiboly was three quarters complete. The somites had taken on a chevron-like shape and resembled muscle myomeres.

Step $E^2$5

Period 24 - 26 days: Completion of epiboly, first appearance of red blood cells, development of vitelline circulation and additional differentiation:

At 24 days, the first muscular contractions were witnessed in the form of periodic tail lashing and wriggling of the trunk and head region. A fairly large rugose area around the embryo interspersed with an incomplete network of shallow grooves and islands marked the expansion of the primordial vitelline circulatory plexus over the yolk. The first established vitelline blood vessels formed a simple loop on either side of the embryo, although no red blood cells were visible (Fig. 31).

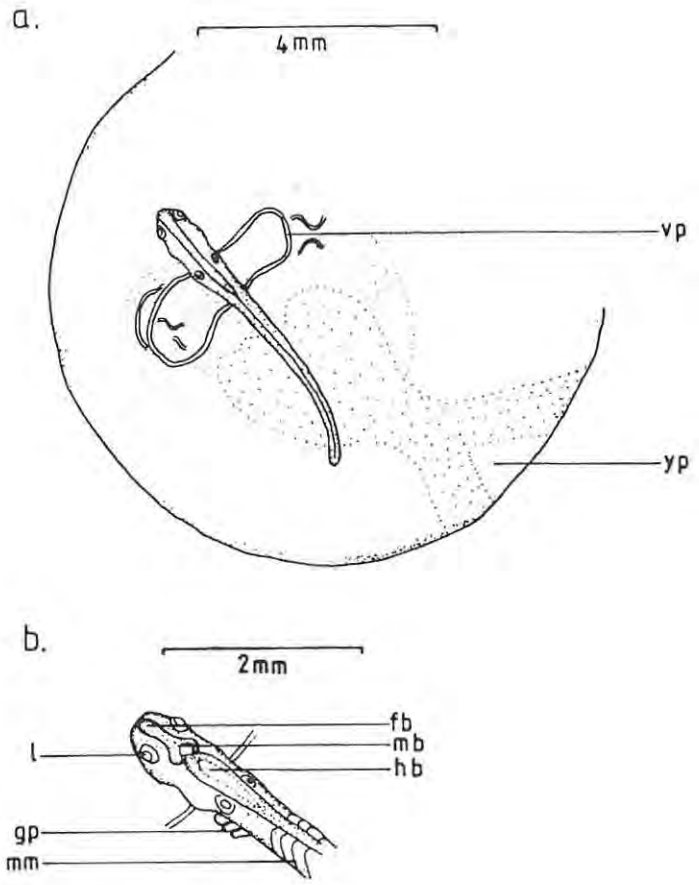


Figure 31. a) Completion of epiboly (24 days), marked by closure of the yolk plug (yp). First appearance of vitelline blood plexus (vp). b) Magnified image of (a) above showing cephalic differentiation into fore- (fb), mid- (mb) and hind-brain (hb). Lenses (l) and 3 pairs of gill pouches (gp) are evident. The somites have taken on the shape of muscle myomeres (mm).

After approximately 25 days, red blood cells were visible for the first time. Large blood sinuses occurred in the vitelline plexus, which had branched considerably and covered approximately one third of the yolk surface. It comprised left and right lateral vitelline veins, arising from the left and right branches of the anterior and posterior cardinal veins, and transported blood from the embryo onto the yolk surface. Here they branched profusely before draining into anterior left and right vitelline veins which returned the blood to the sinus venosus. In addition, the posterior vitelline vein, arising

from the caudal vein, appeared for the first time. Blood vessels were also visible in the embryo, extending anteriorly to the branchial and cranial regions, where blood flow through the branchial arches was evident for the first time, and posteriorly to the tip of the tail. The forebrain had differentiated into two distinct lobes and further invagination and differentiation of the hindbrain had occurred. Dorsal and ventral fin folds were present. The intestine was present as a simple, straight tube (Fig. 32). Embryo length was 7.2mm, head length 1.9mm and postanal trunk length 3.2mm.

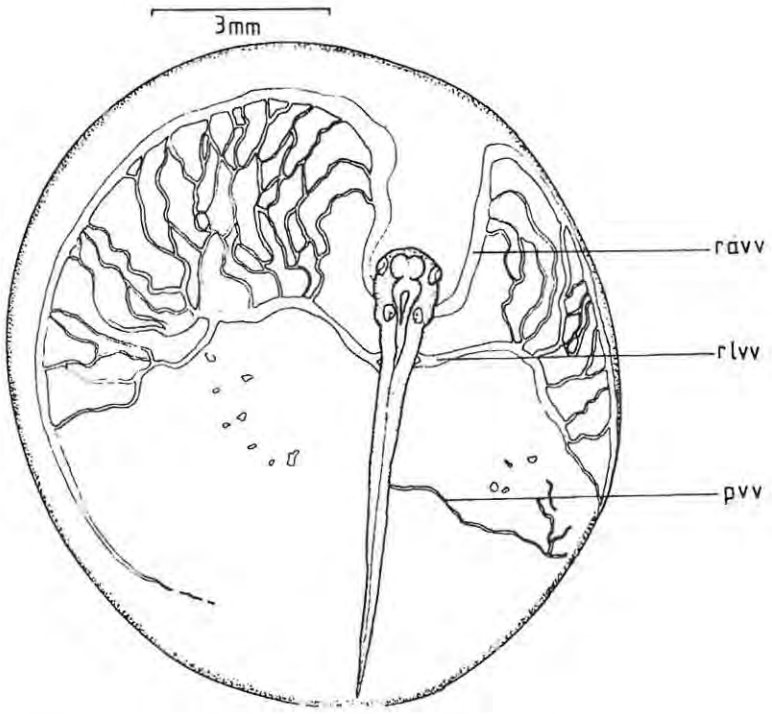


Figure 32. 25 day-old embryo. Note the left and right lateral vitelline veins (rlvv) which radiate extensively before draining into the left and right anterior vitelline veins (ravv) respectively. The posterior vitelline vein (pvv) has begun to differentiate.

StepE^{3}6

Period 27 - 29 days: Vascular proliferation, retinal pigmentation, opening of the mouth and nostrils, appearance of barbel and pectoral fin buds:

After 27 days the eyes had become prominent on either side of the head and the retina had become faintly pigmented. The forebrain lobes were very prominent and were supplied with superficial blood vessels. Maxillary barbel buds were present as were the nasal apertures. Ventrally the rudimentary mouth was open, although incapable of movement, and lead into a highly vascularised tube-gut. Prominent dorsal and ventral intestinal blood vessels were present. A white substance was visible in the intestine. Four gill arches were visible but gill lamellae had not yet formed. An opercular fold, situated anterior to the gill arches had become prominent. The heart was differentiated. The nature of the branchial by-pass system could not be determined due to the opacity of the head region, a phenomenon which obstructed subsequent identification of subcutaneous blood vessels. Hemi-spherical pectoral fin buds were visible for the first time. Considerable vascularisation had occurred in the abdominal region ventral to the notochord, presumed to be the renal plexus, where a network of very fine blood capillaries had resulted in a reddening of the area. A red organ, possibly the presumptive spleen was situated adjacent to the anterior region of the gut. The anterior left and right vitelline veins began to anastomose in the region anterior to the head, a process which lasted between 4 to 5 days before completion. The posterior vitelline plexus had branched and expanded considerably, and the entire vitelline plexus covered approximately half of the yolk surface. The caudal fin fold was pointed, and the notochord straight (Plate VII; Fig. 33). The embryo was 8.9mm long. The head length (to anterior of pectoral fin bud) was 2.0mm. The postanal trunk length was 3.4mm.

From this point onwards, ontogenetic development was recorded using embryos from wild-caught mouth-brooders only.

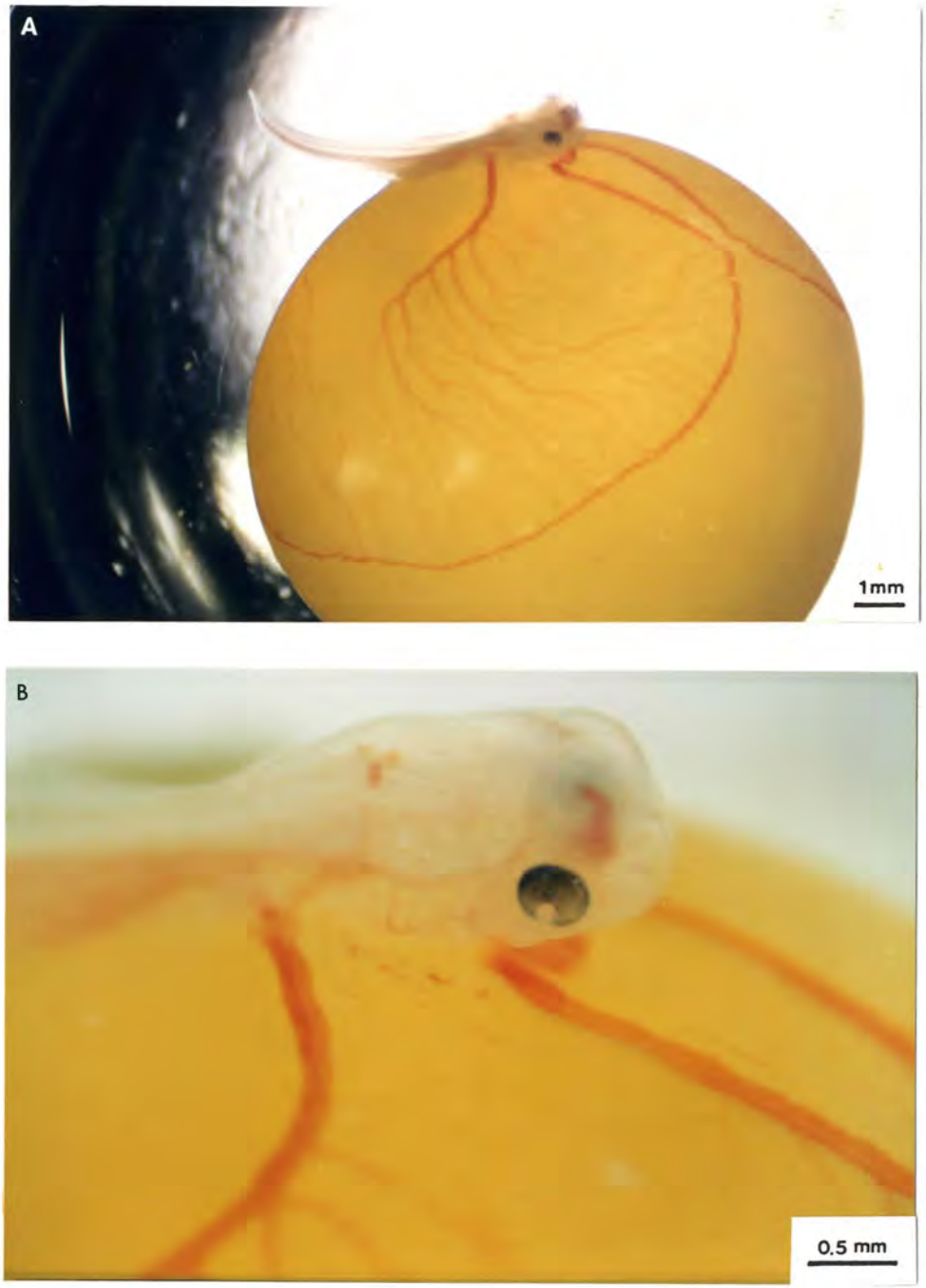


Plate VII. a) Photograph of an embryo (egg envelope removed) at approximately 25 days showing the extent of the vitelline plexus (Mag. 6.6X). b) Higher magnification demonstrating the proliferation of blood vessels in the head and abdomen (25X).

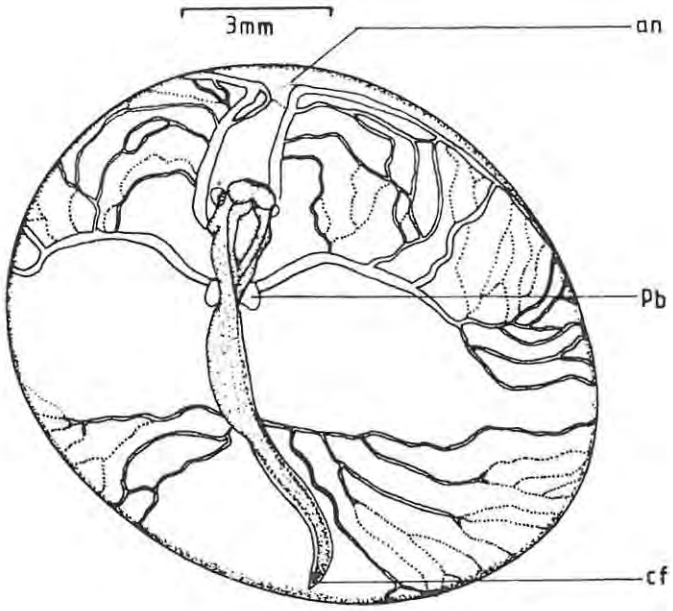


Figure 33. Commencement of anastomosis (an) of anterior left and right vitelline veins (27 days). Expansion of posterior vitelline plexus. Appearance of pectoral fin buds (pb) and retinal pigmentation. Caudal fin-fold (cf) is pointed.

Step $E^{4}7$

Period 30 - 34 days: Notochordal flexion, chondrification of the branchial basket, complete anastomosis of anterior left and right vitelline veins, expansion of posterior vitelline plexus:

After approximately 30 days anastomosis of the anterior left and right vitelline veins was well advanced and the vitelline plexus had expanded considerably. The posterior vitelline circulatory system had linked laterally on the yolk surface with the anterior system for the first time, marking the beginning of the capture of the anterior circulation and the disappearance of the left and right lateral vitelline veins. The highly vascularised presumptive liver was visible adjacent to, and in close association with, the left lateral vitelline vein (hepatic vitelline vein). The notochord had undergone dorsal flexion in the caudal region, and the caudal fin had

taken on a heterocercal shape. The branchial basket showed chondrification for the first time, of four pairs of gill arches. The large lapillus otoliths were prominent. The embryo was 9.9mm long, with a head length of 2.4mm and a postanal trunk length of 3.7mm

After approximately 32 days, the anastomosis of the anterior left and right vitelline veins was complete and the left anterior vitelline vein dominated the flow of blood returning to the heart. As a result of a considerable increase in the size of the presumptive kidney, the renal plexus had become deeply reddened and swollen. The operculum had extended posteriorly and covered the first two gill arches. Dorsal segmental arterioles and venules were visible in the trunk and tail regions. Some of the presumptive pleural ribs were visible as seven lateral vascularised extensions over the yolk. The gall bladder was prominent and was attached to the liver mid-laterally (Fig. 34). The sub-intestinal artery, a branch of the coeliaco-mesenteric artery, was large and prominent and joined the circulation of the inferior caudal vein in the vent region, at the origin of the posterior vitelline vein. The embryo was 11.1 mm long, with a head length of 2.9mm and a postanal trunk length of 4.2mm.

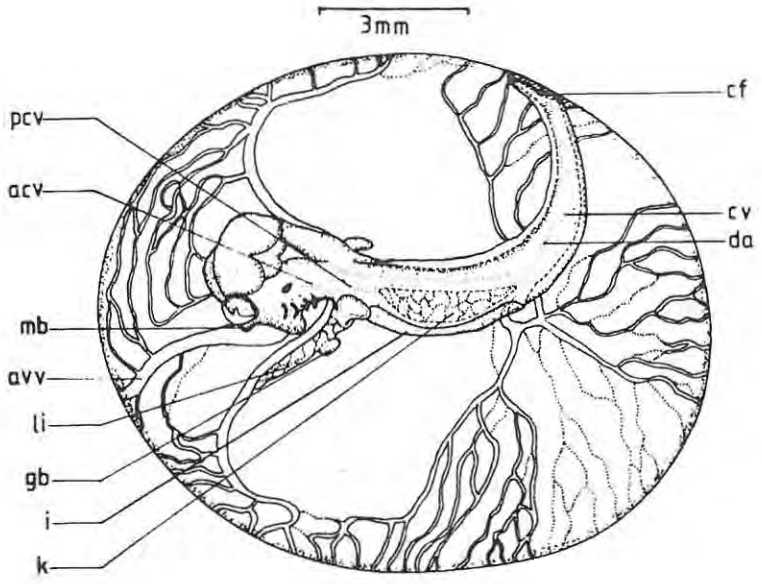


Figure 34. Anastomosis of left and right anterior vitelline veins (32 days) has resulted in a single anterior vitelline vein (avv). The anterior (acv) and posterior cardinal veins (pcv) unite to form the lateral vitelline veins. The dorsal aorta (da) and caudal vein (cv) are prominent. The posterior vitelline plexus has expanded considerably and has linked up laterally with the anterior vitelline plexus. Considerable vascularisation in the vicinity of the presumptive kidney (k). Intestine (i) a simple tube. Presumptive liver (li) and gall bladder (gb) developing in close association with left lateral vitelline vein (also known as hepatic vitelline vein). Maxillary barbel buds (mb) and an opercular fold are prominent. Four gill arches visible. Caudal fin heterocercal in shape.

Step $E^5 8$

Period 35 - 54 days: First ossification, fin differentiation, increased branchial circulation, loss of lateral left and right vitelline veins, first pigmentation, appearance of swim bladder:

After approximately 35 days the maxillary barbels had elongated and protruded posteriorly beyond the eyes. The operculum had extended posteriorly and covered the first two gill arches. The subclavian veins were visible in the pectoral fin buds, which had become slightly pointed posteriorly. The intestine

had developed a slight bend anteriorly, indicating an increase in length and the onset of the stomach differentiation. Ossification was evident for the first time. The left and right cleithra had begun ossification, marking the pectoral girdle as the area of earliest skeletal maturation (Fig. 35). Meckels cartilage was prominent and the notochord was strongly cartilaginous. Embryo length was 11.1mm, head length 2.9mm and postanal trunk length 4.8mm.

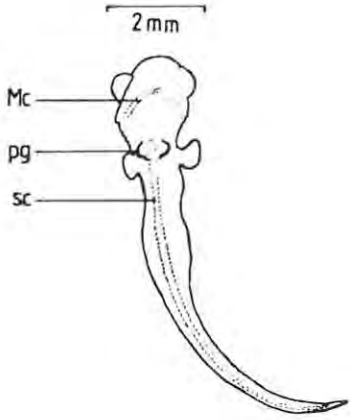


Figure 35. Ventral view of stained and cleared specimen (35 days) showing first ossification in the pectoral girdle (pg). Meckels cartilage (Mc) and spinal column sc) well chondrified.

After approximately 38 days the anastomosis of the left and right anterior vitelline veins on the ventral aspect of the yolk was complete, and the single sub-intestinal vitelline vein now collected and transported blood anteriorally to the duct of Cuvier and the heart. The position of the gall bladder had changed. It was now situated ventral to the antero-laterally directed liver and contained a green substance, presumably bile. The dorsal fin fold had become enlarged in the region of the presumptive dorsal fin. The circulation in the caudal area had become more elaborate with the addition of ventrally directed loops, heralding the beginning of the homocercal caudal condition. The pectoral fin buds had elongated considerably in a posterior direction. The regions of the brain were well defined and a complex network of cutaneous blood vessels was visible on the head. The large lapillus otoliths

were distinct in the otic capsule (Plate VIIIa & b). The operculum covered three of the branchial arches. The fully formed mouth opened and closed synchronously with opercular movements. The mandibular barbels were elongate. Embryo length 12.2mm, head length 2.9mm, and postanal trunk length 5.9mm.

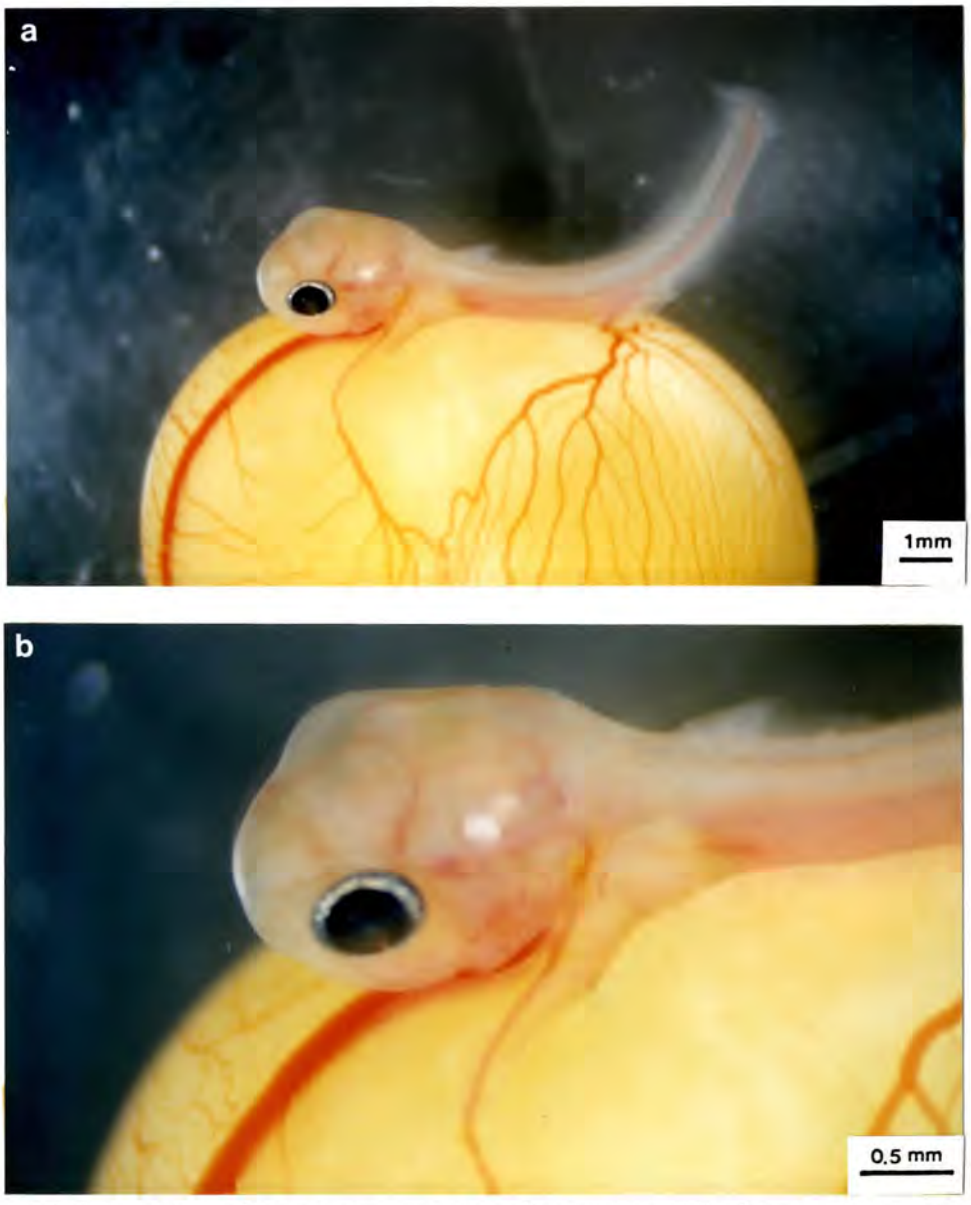


Plate VIII. a) Embryo at approximately 38 days (egg envelope removed) showing differentiation of the dorsal and anal fins from the fin folds. Caudal fin shows early homocercal condition. The posterior vitelline plexus has joined with the anterior vitelline plexus laterally and now carries most of the vitelline blood (6.6X). b) Higher magnification (25X) showing the proliferation of cutaneous blood vessels on the head, prominent lapillus otoliths and reduction in size of left lateral vitelline vein.

Two days later, at approximately 40 days, pectoral, dorsal and caudal fin lepidotrichia were visible for the first time. The operculum had completely covered the gill arches and the heart was nestled between the posterior-most left and right pair. Some differentiation of the stomach was visible as an L-shaped convolution in the anterior region of the gut. The white substance in the intestine extended approximately halfway to the vent. The swim bladder was visible for the first time, nestled anterior to the kidney, dorsal to the stomach. A yellow pigmented organ was visible in the coelomic cavity situated to the right of and adjacent to the stomach, probably the spleen. The liver was large and anteriorly directed lateral to the embryo, extending anterior to the heart. The spherical gall bladder was filled with bile. Dark pigmentation began to appear on the ventral surface of the kidney. What may have been rudimentary gonad material was visible as paired threads running medio-ventrally to the kidney, ending near the vent.

After 43 days, melanophores appeared on the head for the first time, being concentrated over the optic lobe and cerebellar areas. Simple olfactory rosettes were visible through the olfactory nares. The pectoral and dorsal spines and rays were differentiating. The pelvic fin buds had appeared. More of the blood from the caudal vein began flowing into the posterior cardinal vein, largely by-passing the posterior vitelline vein and the vitelline respiratory complex. The left lateral vitelline vein (hepatic vitelline vein) had moved medio-laterally underneath the embryo together with the liver. The hepatic vein now lead directly into the duct of Cuvier. The right lateral vitelline vein had also decreased in size, indicating that some of the blood from the right anterior and posterior cardinal veins was flowing directly into the ductus Cuvieri for the first time (Fig. 36).

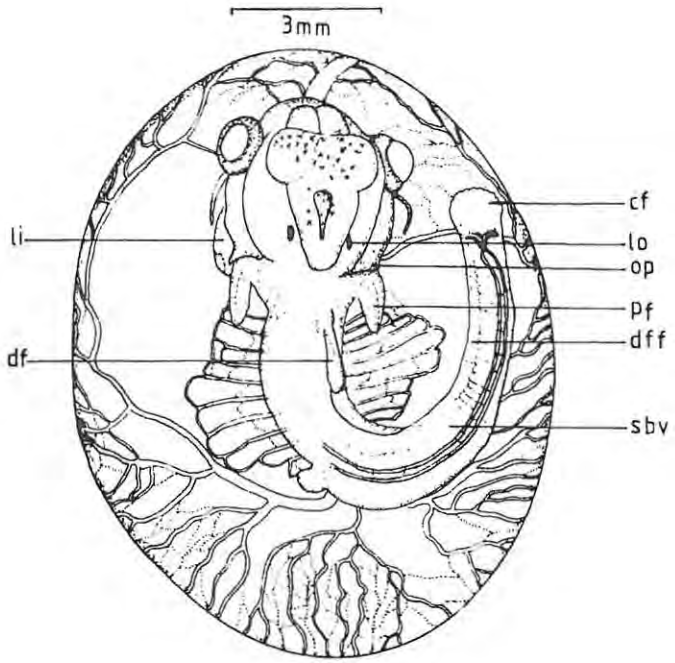


Figure 36. The left anterior vitelline vein has moved anteromedially underneath the embryo along with the liver (43 days), and no longer serves a respiratory function. Right lateral vitelline vein reduced in size. Posterior vitelline plexus now dominant. Segmental blood vessels (sbv) prominent. Vascularisation of dorsal fin fold (dff). Advanced differentiation of the brain. Lapillus otoliths (lo) large. Operculum complete, pectoral (pf), dorsal (df) and caudal fins (cf) rayed. Caudal fin fully homocercal.

In one embryo, blood in the right lateral vitelline vein was seen to have reversed its flow, carrying blood from the vitelline plexus into the embryo. This may however have arisen as a result of damage to the vitelline circulatory system during handling. The by-passing of the vitelline circulation system was an indication that the gills were actively involved in respiration. However, examination of the gills revealed the presence of short, stumpy primary lamellae only. There were no secondary lamellae present.

Ossification was evident proximally in the pectoral and dorsal spines and pterygiophores, in the operculae, dentary, the four

outermost branchiostegals, the maxillae and the centra of all the vertebrae excepting the caudal-most three (Fig. 37; Table XI). The embryo was 13.9mm long. The head length was 3.0mm and the postanal trunk length was 6.9mm.

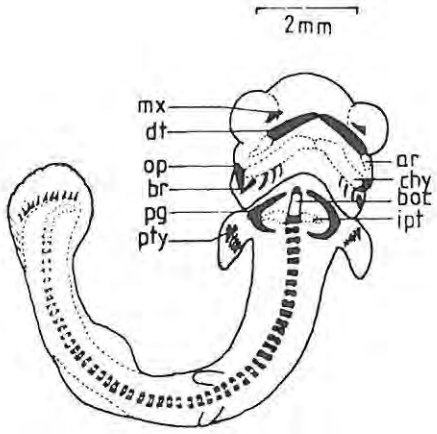


Figure 37. Ventral view of stained and cleared specimen (43 days) showing degree of ossification. Pectoral girdle (pg), dentary (dt), maxillae (mx), operculae (op), 4 pairs of branchiostegal rays (br), vertebral centra, dorsal, pectoral and caudal fin pterygiophores (pty). Basi-occipital (bo) partly ossified. Ceratohyal (chy) and articular (ar) chondrified.

After approximately 50 days, lepidotrichia appeared in the pelvic fins. Dorsally, pigmentation extended laterally to the eyes and posteriorly to the nape region. Segmental arterioles and venules were prominent in the dorsal and ventral fin folds posterior to the differentiated dorsal and anal fins. Additional ossification appeared in the superior limb of the post-temporal, interopercular, frontal, parasphenoid and exoccipital. All the vertebral centra showed some ossification. The pre-anal vertebrae showed ossification of the neural and haemal spines.

Table XI: Summary of the degree of skeletal ossification during step $E^5 8$, after approximately 43 days.

	DEGREE OF OSSIFICATION			
	NONE	SLIGHT	MODERATE	ADVANCED
Pectoral spine		*		
Pectoral fin pteryglophores		*		
Cleithrum- ventral limb				*
post humeral process		*		
Ceratohyal		*		
Hypohyal		*		
Epihyal	*			
Urohyal	*			
Branchiostegals			*	
Dentary			*	
Operculum				*
Preopercle		*		
Interopercle		*		
Hyomandibular	*			
Quadrate	*			
Metapterygoid	*			
Vertebral centra		*		
Vertebral spines		*		
Fused vertebral complex		*		
Transverse process 4th vertebra		*		
Weberian ossicles		*		
DORSAL NEUROCRANIAL SKELETON				
Dermosupraoccipital	*			
Pterotic	*			
Sphenotic		*		
Post temporal		*		
Sup. post temporal		*		
Pre-frontal		*		
Frontal	*			
Maxillary		*		
Dermethmoid		*		
VENTRAL NEUROCRANIAL SKELETON				
Inf. post temporal		*		
Basioccipital		*		
Pro-otic	*			
Parasphenoid		*		
Orbitosphenoid		*		
Prevomer	*			
Vomer		*		
CAUDAL SKELETON				
Preural centra		*		
Uronural	*			
Parhypural		*		
Hypurals	*			
Caudal pteryglophores			*	

Step $E^6 9$

Period 55 - 75 days: Growth, skeletal ossification, lateral line development and dermal pigmentation after completion of fin differentiation:

Pigmentation was extensive after approximately 55 days, covering the entire cranial, nape and trunk areas, reaching the caudal peduncle. Few subdermal features were subsequently visible. The eyes had become surrounded by cranial and neurocranial elements and were no longer prominent on either side of the head. The full compliment of pterygiophores was present in both the paired and unpaired fins. The dorsal and ventral fin folds were prominent and well vascularised. The embryo was large and the trunk region was recurved so that the caudal fin was situated anteriorly, adjacent to the head (Fig. 38).

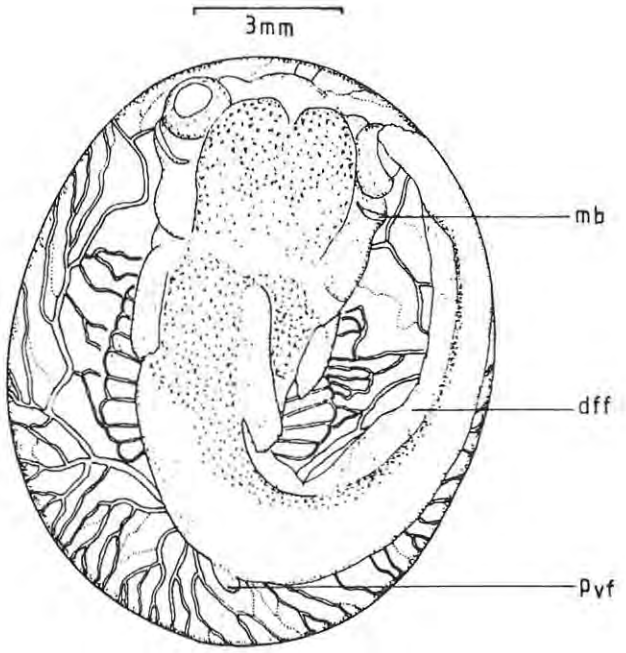


Figure 38. Dorsal view of an embryo after approximately 55 days. Differentiation of pelvic fin (pvf) marks the completion of fin differentiation. Considerable pigmentation of dorsal regions of head, nape and trunk. Vitelline circulation completely dominated by the posterior vitelline plexus. Dorsal (dff) well vascularised. Maxillary (mb) and mandibular barbels fully formed.

Lateral line vesicles were present on the head, extending to the posterior margin of the cleithrum. The head lateral line was represented by a single anteriorly directed dorso-lateral branch on either side of the head, extending above the eye and ending medially to the nostril, at the premaxilla. Embryo length 18.8mm, head length 3.8mm and postanal trunk length 10.0mm. Ossification proceeded rapidly during this period and the degree of ossification is presented in Figure 39 and Table XII.

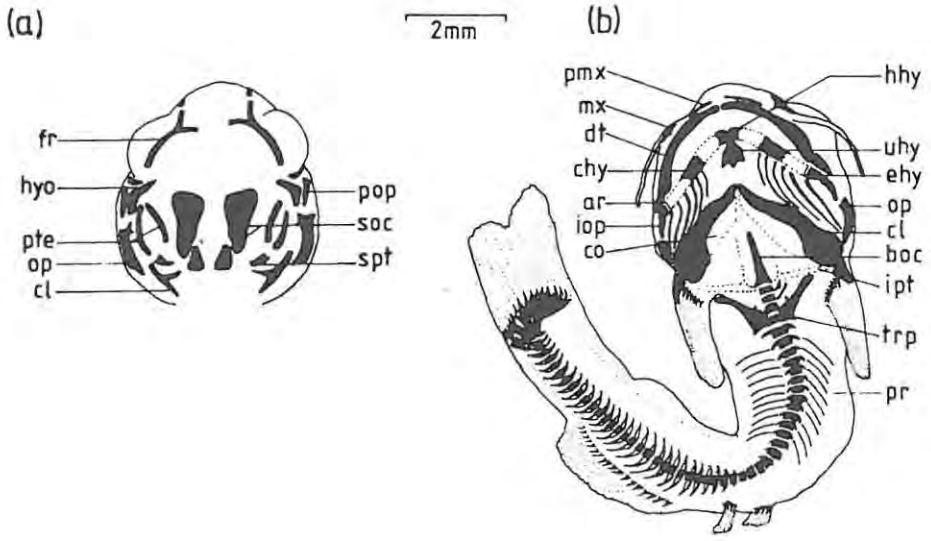


Figure 39. a) Dorsal view of stained and cleared specimen (± 55 days) illustrating the degree of ossification (represented by blackened areas). Supra-occipital (soc), supra-post-temporal (spt), cleithrum (cl), pterotic (pte), operculum (op), pre-operculum (pop), hyomandibular (hyo) and frontal (fr) well ossified. b) Ventral view: Maxillae (mx), pre-maxillae (pmx), dentary (dt), articular (ar), hypohyal (hhy), epihyal (ehy), 6 pairs of branchiostegal rays (br), cleithrum (cl), basi-occipital (bo), transverse process of 4th vertebral centrum (trp), pleural ribs (pr) and neural and haemal vertebral arches. Ceratohyal (chy), coracoid (co), inferior post-temporal (ipt) and caudal skeleton incompletely ossified.

Table XII: Degree of skeletal ossification during step $E^{6}9$, just prior to hatching (approximately 65 days).

	DEGREE OF OSSIFICATION			
	NONE	SLIGHT	MODERATE	ADVANCED
PECTORAL & NEURAL SKELETON				
Pectoral spine		*		
Pectoral fin pteryglophores		*		
Cleithrum - ventral limb				*
- post humeral process		*		
Ceratohyal			*	
Hypohyal			*	
Epihyal		*		
Urohyal			*	
Branchiostegals				*
Dentary				*
Operculum				*
Preopercle				*
Interopercle				*
Hyomandibular		*		
Quadrate		*		
Metapterygoid		*		
Vertebral centra			*	
Vertebral spines			*	
Fused vertebral complex			*	
Transverse process 4th vertebra			*	
Weberian ossicles			*	
DORSAL NEUROCRANIAL SKELETON				
Dermosupraoccipital		*		
Pterotic		*		
Sphenotic			*	
Post temporal		*		
Sup. post temporal		*		
Pre-frontal			*	
Frontal		*		
Nasal				*
Dermethmoid		*		
VENTRAL NEUROCRANIAL SKELETON				
Inf. post temporal		*		
Basioccipital		*		
Pro-otic		*		
Parasphenoid		*		
Orbitosphenoid		*		
Prevomer		*		
Vomer	*			
CAUDAL SKELETON				
Preural centra			*	
Uronural				*
Parhypural			*	
Hypurals		*		
Caudal pteryglophores				*

After approximately 65 days pigmentation was dense and covered the entire dorsal surface including the fins, where it was less densely distributed. The dorsal and ventral fin-folds were devoid of pigmentation. The digestive tract was still largely undifferentiated. The pyloric sphincter was present

and the stomach was still L-shaped. The intestine was a simple, straight tube through to the vent. The liver had increased in size but still had only a single lobe and the spleen was large and orange in colour. The primary lamellae on the gill arches had elongated and secondary lamellea were clearly visible. The swim bladder was nestled between the kidney and the head kidney and was dumb-bell shaped. The embryo had grown considerably in length and in girth. The total length was 24.2mm, head length 4.3mm and post anal trunk length 13.2mm.

Several days prior to hatching the embryo appeared extremely constricted within the vitelline membrane, being doubled over with the caudal fin extended over and beyond the head. The heavily vascularised dorsal and ventral fin folds were still prominent. The vitelline plexus, now originating entirely from the posterior vitelline vein, was profusely branched and a fine network of capillaries, covering the entire yolk-sac, was interspersed between the larger vessels (Fig. 40).

Summary of the vitelline circulatory development

The left and right lateral vitelline veins arise from the paired anterior and posterior cardinal veins which meet and flow adjacent to one another laterally over the yolk for a short while before branching into a complex network of capillaries. These capillaries eventually collect into the large left and right anterior vitelline veins, which meet just prior to entering the sinus venosus and the heart. The return flow from the caudal peduncle is via the caudal vein. While most of the blood from the caudal vein flows into the posterior vitelline vein (which later becomes the sub-intestinal vein), some also enters the posterior cardinal vein. Later in the development, the blood flow from the caudal vein is re-routed and flows primarily into the posterior cardinal vein, which in turn drains into the duct of Cuvier. The intestinal and gastric veins lead into the liver via the hepatic portal system, and the hepatic vein carries blood from the liver into sinus venosus and the heart.

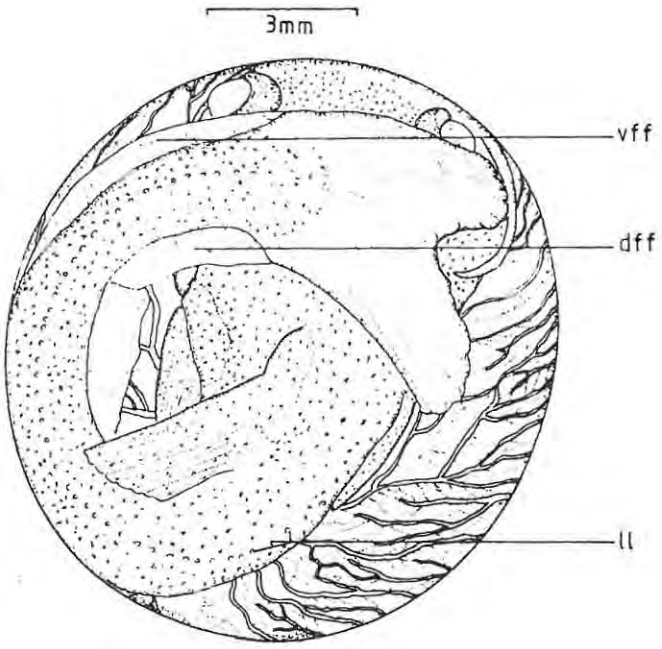


Figure 40. Embryo shortly before hatching (± 70 days). Extremely profuse posterior vitelline plexus, well vascularised dorsal (dff) and ventral fin folds (vff), dense pigmentation throughout, lateral line (ll) prominent. Embryo large and constricted within egg envelope, caudal peduncle and fin doubled back and situated dorsal to the head

The left and right anterior vitelline veins anastomose in the region immediately anterior to the head after approximately 27 days, resulting in blood flow being redirected (after approximately 30 - 31 days), to the left anterior vitelline vein, which expands to accommodate the drainage from the entire vitelline plexus. As the vitelline network expands the anastomoses of the two branches of the anterior vitelline vein continues in a zip-like fashion in the mid-antero and subsequently mid-ventral plane (Plate IX), until the entire yolk is completely enveloped by the vitelline plexus.

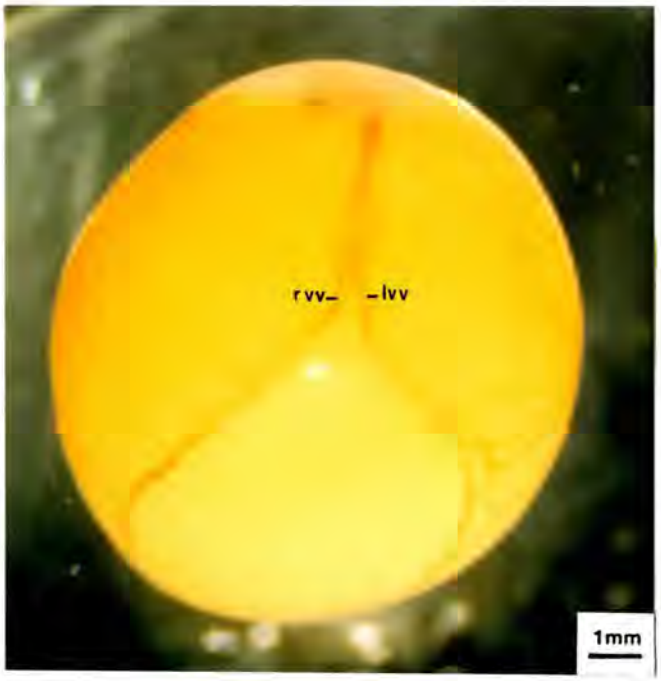


Plate IX. Antero-ventral aspect of an embryo (± 30 days) demonstrating the progressive anastomosis of the anterior left (lvv) and right (rvv) vitelline veins in a ventral direction.

The completion of this anastomosis results in the formation of a single sub-intestinal vitelline vein. At this stage the left lateral vitelline vein (hepatic vitelline vein) has disappeared from view along with the liver which has moved antero-medially inwards and underneath the embryo. The blood flow in the right lateral vitelline vein becomes captured by, and incorporated into, the expanding posterior vitelline vein network and also disappears. The anterior and posterior cardinal veins, which initially fed the right lateral vitelline vein, now flow into the hepatic portal system and the duct of Cuvier respectively. A few days later, some of the blood from the caudal vein by-passes the posterior vitelline plexus and is re-routed into the posterior cardinal vein. This may be indicative of the completion of the branchial circulatory system. The posterior vitelline plexus continues to proliferate, however, and forms a dense network of capillaries around the entire yolk-sac

lead into the sub-intestinal vitelline vein. The vitelline plexus is finally enveloped by the expanding ventral body wall.

Free-embryo phase

Step $F^{1}10$

Period 75 - 100 days: Hatching, straightening of the trunk region, more growth and ossification, continued differentiation of the digestive system and the onset of exogenous feeding:

Hatching occurred after approximately 75 to 80 days, as evidenced by the ejection of egg envelopes from the buccal cavity in aquarium-held mouth-brooders. Embryos hatched head-first through a tear in the egg envelope which commenced in the region immediately dorsal to the head. The dorsal and ventral fin folds in the caudal region were still present at hatching. The lateral line extended from the caudal peduncle to the head where it branched and completely encircled the eye and nostril. Additional branches extended anteriorly across the frontal to the upper lip, postero-dorsally across the pterotic and medially across the sphenotic. The left and right branches on the head did not meet, however. The stomach had differentiated and resembled the adult U-shape. The intestine exhibited considerable elongation and was thrown into two loops, one beneath the stomach and the other posteriorly, near the vent. The swim bladder differentiation was complete and the characteristic heart shape had been reached. The pneumatic duct was large and entered the oesophagus antero-ventrally to the swim bladder. The primary lamellae on the gill arches were considerably elongated, although they appeared on only four of the gill arches. Total length at hatching was 32.5mm (± 1.5mm, n = 35). Head length 5.8mm, postanal trunk length 15.9mm.

Ossification of the skeleton was moderately advanced. All skeletal elements were at least partly ossified, with the exception of the pleural ribs (Table XIII; Fig. 41).

Table XIII: Skeletal ossification during step F[1]10, immediately following hatching (Approximately 80 days).

	DEGREE OF OSSIFICATION			
	NIL	SLIGHT	MODERATE	ADVANCED
PECTORAL & NEURAL SKELETON				
Pectoral spine			*	
Pectoral fin pterygiophores				*
Cleithrum - ventral limb				*
Cleithrum - post humeral process			*	
Ceratohyal			*	
Hypohyal				*
Epihyal		*		
Urohyal			*	
Branchiostegals				*
Dentary				*
Operculum				*
Preopercle				*
Interopercle				*
Hyomandibular			*	
Quadrate				*
Metapterygoid			*	
Vertebral centra				*
Vertebral spines				*
Fused vertebral complex			*	
Transverse process 4th vertebra			*	
Weberian ossicles			*	
DORSAL NEUROCRANIAL SKELETON				
Dermosupraoccipital			*	
Pterotic		*		
Sphenotic				*
Post temporal			*	
Sup. post temporal			*	
Pre-frontal			*	
Frontal		*		
Maxillary			*	
Dermethmoid		*		
VENTRAL NEUROCRANIAL SKELETON				
Inf. post temporal				*
Basioccipital				*
Pro-otic			*	
Parasphenoid			*	
Orbitosphenoid			*	
Prevomer				*
Vomer				*
CAUDAL SKELETON				
Preural centra				*
Uronural				*
Parhypural			*	
Hypurals		*		
Caudal pterygiophores				*

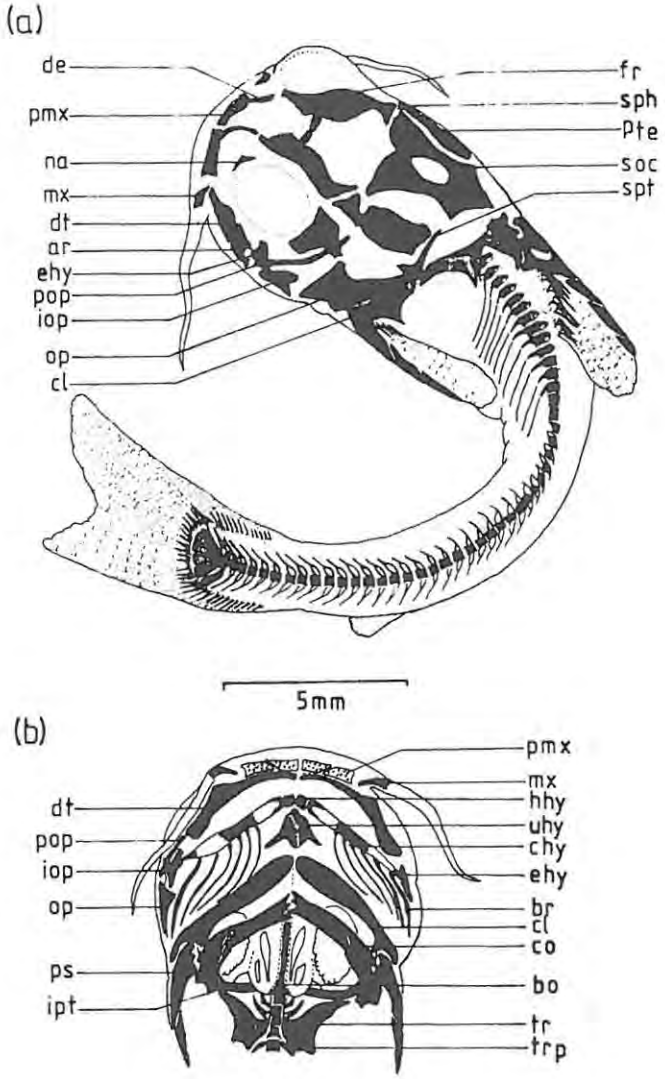


Figure 41. a) Dorso-lateral view of cleared and stained specimen (± 90 days): Premaxilla (pmx), dermethmoid (de), maxilla (mx), frontal (fr), articular (ar), nasal (na), sphenotic (sph), pterotic (pte), supra-occipital (soc), hyomandibular (hyo), epihyal (epy), interopercle (iop), preopercle (pop), operculum (op), cleithrum (cl), superior post-temporal (spt), dorsal and pectoral spines. Caudal skeleton incompletely ossified. b) Ventral view of head region: Premaxillae (pmx) and dentary with teeth, maxillae (mx), hypohyal (hhy), urohyal (uhy), ceratohyal (chy), epihyal (epy), coracoid (co), basi-occipital (bo), inferior post-temporal (ipt), pectoral spine (ps). Lapillus, sagittal and astericus otoliths prominent. Weberian ossicles incompletely arranged. Tripus (tr) prominent.

The size of the free-embryo yolk-sac at hatching was considerable (Fig. 42), and was found to severely limit their swimming ability.

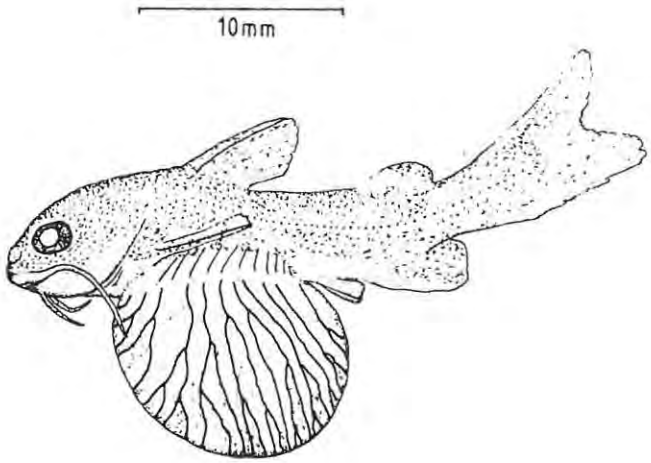


Figure 42. Lateral view of a free-embryo shortly after hatching (± 90 days), showing full differentiation of all external structures. The yolk-sac is large and well vascularised.

Step $F^2$11

Period 100 - 140 days: Completion of skeletal ossification, more growth, absorption of yolk-sac, elaboration of lateral line system, intensification of pigmentation and release from the buccal cavity:

After approximately 110 days, the ventral body wall had grown halfway around the yolk-sac. The dorsal and ventral fin folds had disappeared and the embryo had darkened in colour. Internally the liver had increased considerably in size and occupied the area anterior and dorsal to the stomach. Dorsally it abutted against the greatly enlarged swim bladder. Food particles were evident in the stomach while the intestine had elongated considerably to form several loops within the abdominal cavity. At 27mm it was approximately two-thirds of the free embryo length (44mm TL), (Fig. 43).

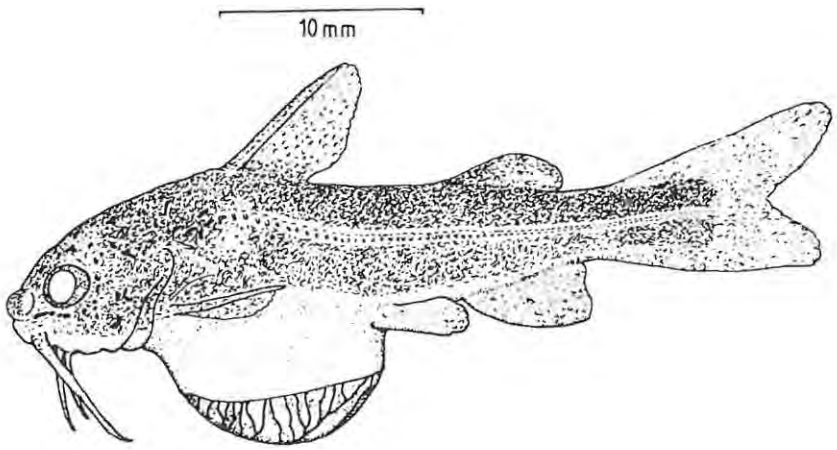


Figure 43. Lateral view of a free-embryo after approximately 120 days showing advanced absorption of yolk-sac and proliferation of the head lateral line.

Release of juveniles occurred once the yolk sac had been totally absorbed and the ventral body wall had knitted, after approximately 140 days. Total length at release was 54.3mm (± 2.0mm, n = 50). Traces of yolk were still visible internally, around the viscera. The juveniles were morphologically similar to the adults at this time although structures such as the olfactory rosettes, secondary gill lamellae and head lateral line were incompletely developed, and would not show complete development until sexual maturity (Fig. 44).

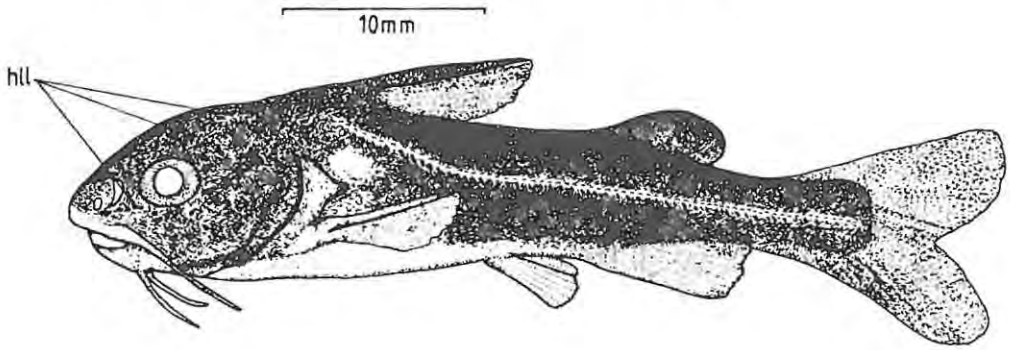


Figure 44. Lateral view of a juvenile G. feliceps at time of release from the adult buccal cavity (± 140 days). Pigmentation is dense, yolk-sac completely absorbed and head lateral line (hll) more extensive.

Skeletal ossification at the time of liberation was almost complete. The only bones still exhibiting some cartilaginous material were in the cranium and neurocranium (Table XIV; Fig. 45).

Table XIV: Degree of ossification at the time of release from the adult buccal cavity (Approximately 140 days).

	DEGREE OF OSSIFICATION			
	NONE	SLIGHT	MODERATE	ADVANCED
PECTORAL & NEURAL SKELETON				
Pectoral spine				*
Pectoral fin pterygiophores				*
Cleithrum - ventral limb				*
- post humeral process				*
Ceratohyal				*
Hypohyal				*
Epihyal			*	
Urohyal			*	
Branchiostegals				*
Dentary				*
Operculum				*
Preopercle				*
Interopercle				*
Hyomandibular				*
Quadrate				*
Metapterygoid				*
Vertebral centra				*
Vertebral spines				*
Fused vertebral complex				*
Transverse process 4th vertebra				*
Weberian ossicles				*
DORSAL NEUROCRANIAL SKELETON				
Dermosupraoccipital			*	
Pterotic			*	
Sphenotic				*
Post temporal			*	
Superior post temporal				*
Pre-frontal			*	
Frontal			*	
Maxillary			*	
Dermethmoid				*
Palatine		*		
VENTRAL NEUROCRANIAL SKELETON				
Inf. post temporal				*
Basioccipital				*
Pro-otic			*	
Parasphenoid				*
Orbitosphenoid			*	
Prevomer		*		
Vomer			*	
CAUDAL SKELETON				
Preural centra				*
Uronural				*
Parhypural				*
Hypurals			*	
Caudal pterygiophores				*

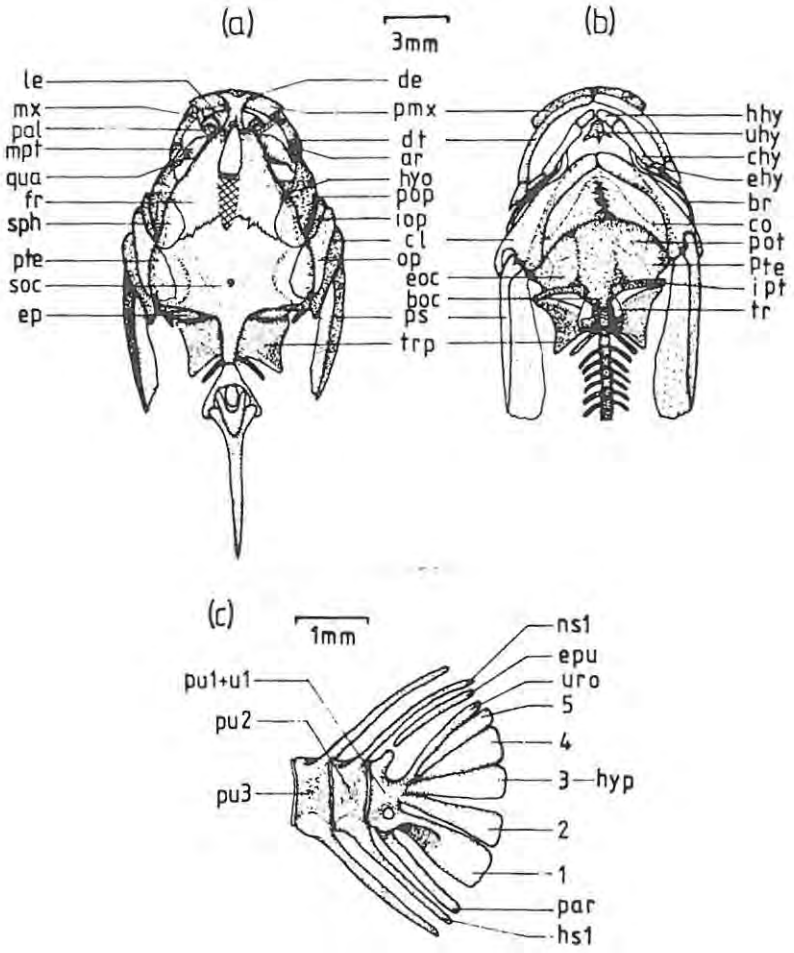


Figure 45. Prepared dry skeleton of a juvenile at time of release (± 140 days). a) Dorsal view of head region: Lateral ethmoid (le), dermethmoid (de), maxillae (mx), premaxillae (pmx), dentary (d), palatine (pal), articular (ar), metapterygoid (mpt), quadrate (qua), hyomandibular (hyo), frontal (fr), pre-opercular (pop), inter-opercular (iop), frontal (fr), sphenotic (sph), pterotic (pte), supra-occipital (soc), cleithrum (cl), opercular (op), epiotic (ep), transverse process of 4th fused vertebra (trp). b) Ventral view: Hypohyal (hhy), urohyal (uhy), ceratohyal (chy), epihyal (ehy), 6 prs. branchiostegal rays (br), coracoid (co), pro-otic (pot), pterotic (pte), inferior post-temporal (ipt), basioccipital (boc), exoccipital (eoc), tripus (tr). c) Caudal skeleton: Pre-ural centra (pu2, pu3), fused complex ural centrum (pu1 + u1), first neural spine (ns1), epural (epu), uronural (uro), hypurals (hyp 1-5), parhypural (par), first haemal spine (hs1).

Artificial fertilisation and incubation of G. feliceps eggs and embryos together with evidence gleaned from a series of wild-caught broods indicated that the incubation period up to the time of hatching was in the region of 75 to 80 days. The incubation time subsequent to hatching was less clear. Field evidence demonstrated that the size of embryos at release from the adult buccal cavity was approximately 54mm (± 5mm, n = 53). Aquarium-held mouth-brooders demonstrated an incubation period between hatching and release from the buccal cavity of exactly 65 days (n = 2). Approximately 21 days after hatching the adult fish showed an interest in and ingested food for the first time, marking the onset of exogenous feeding by the free-embryos. Free-embryos held in the incubators were fed regularly from the time of hatching and reached the 'release length' after approximately 35-45 days, 20 days earlier than mouth-brooded free-embryos. This indicated that the super abundance of exogenous food available to the incubator-reared free embryos might have artificially accelerated their growth rate. The youngest embryos that were incubated by aquarium-held mouth-brooders were, using the data from artificially fertilised and incubated embryos, estimated to be approximately 14 days old at capture. The incubation times through to release of young in these mouth-brooders (n = 2), was 129 and 131 days respectively. This was representative of a total incubation period between fertilisation and release of young of approximately 143-145 days.

The batches of embryos being incubated by the two mouth-brooders referred to above were judged to be the same age at the time of capture. Notably, in these two mouth-brooders, both hatching (evidenced by the ejected egg envelopes seen in the aquarium) and release of young occurred exactly two days earlier in the one individual than it did in the other. This was an indication that, under the particular set of environmental conditions present in the laboratory, ontogenetic development in G. feliceps proceeded at a very definite rate.

The growth in total, head and postanal trunk length, between the 20th day (25 somite stage) and the time at release from the buccal cavity (± 140 days) is presented in Figure 46. The early ontogeny was marked by irregular growth until approximately the 50th day (coinciding with the completion of differentiation), after which it was consistent. The relatively few data points used in the construction of the curves may have resulted in artificially smooth growth rates.

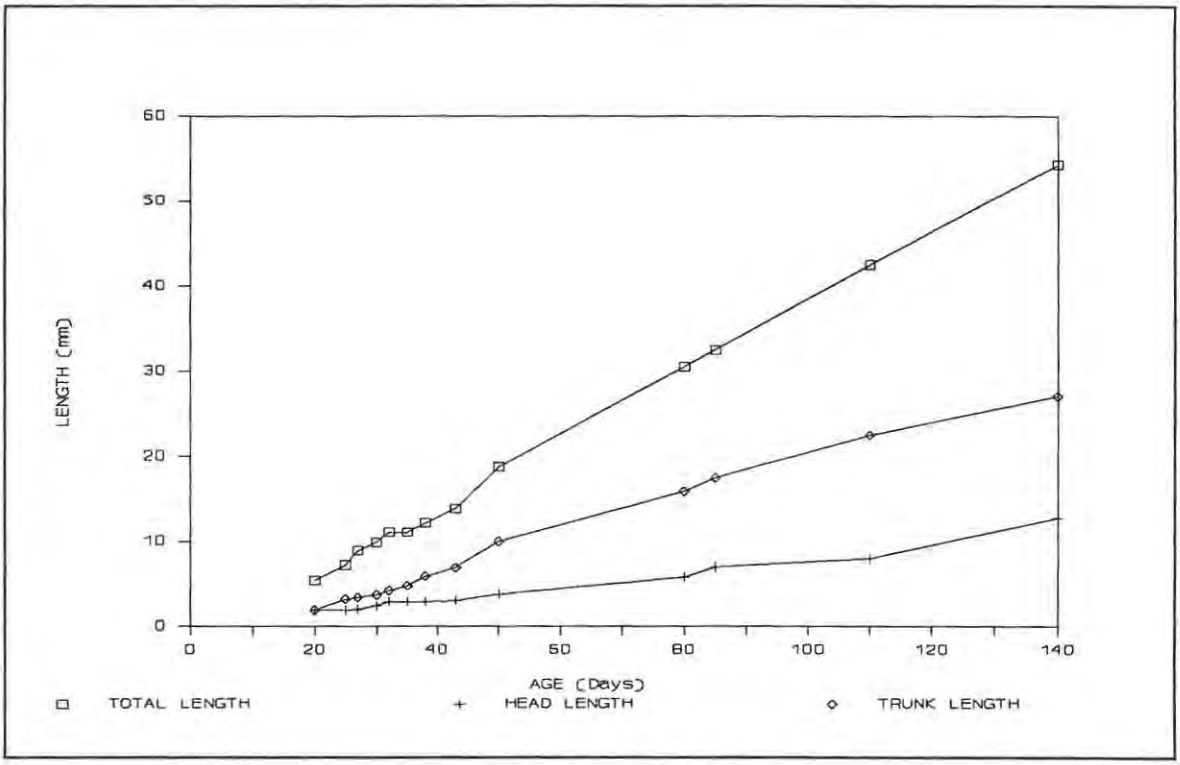


Figure 46. Growth in total, head and postanal trunk length between day 20 and day 140. Growth was irregular until approximately the 50th day, coinciding with the completion of differentiation, after which it was consistent.

The changes in adult ventilation rates associated with mouth-brooding are graphically presented in Figure 47. Ventilation rates did not change gradually over time in accompaniment with embryonic development. They were relatively constant for the duration of the embryonic phase and then exhibited a sudden, significant decline after hatching (adjusted Chi-sq.= 8.605,

df=1, P > 0.01), (the ventilation rate of the non-brooding, actively feeding control animals was used as the expected value in the contingency table for the Chi-Square test). This decline was probably enabled by an increased oxygen availability to the free-embryos after shedding of the egg envelope, a former barrier to oxygen diffusion. Also, the embryonic branchial respiratory apparatus was functional at hatching, enabling maximal oxygen extraction from the incurrent water in the parent buccal cavity. As the ventilation rate of mouth-brooders carrying free-embryos was significantly lower than that of control animals, this was also indicative of a much lower metabolic oxygen requirement (for basal metabolism) during buccal incubation than during periods of active feeding.

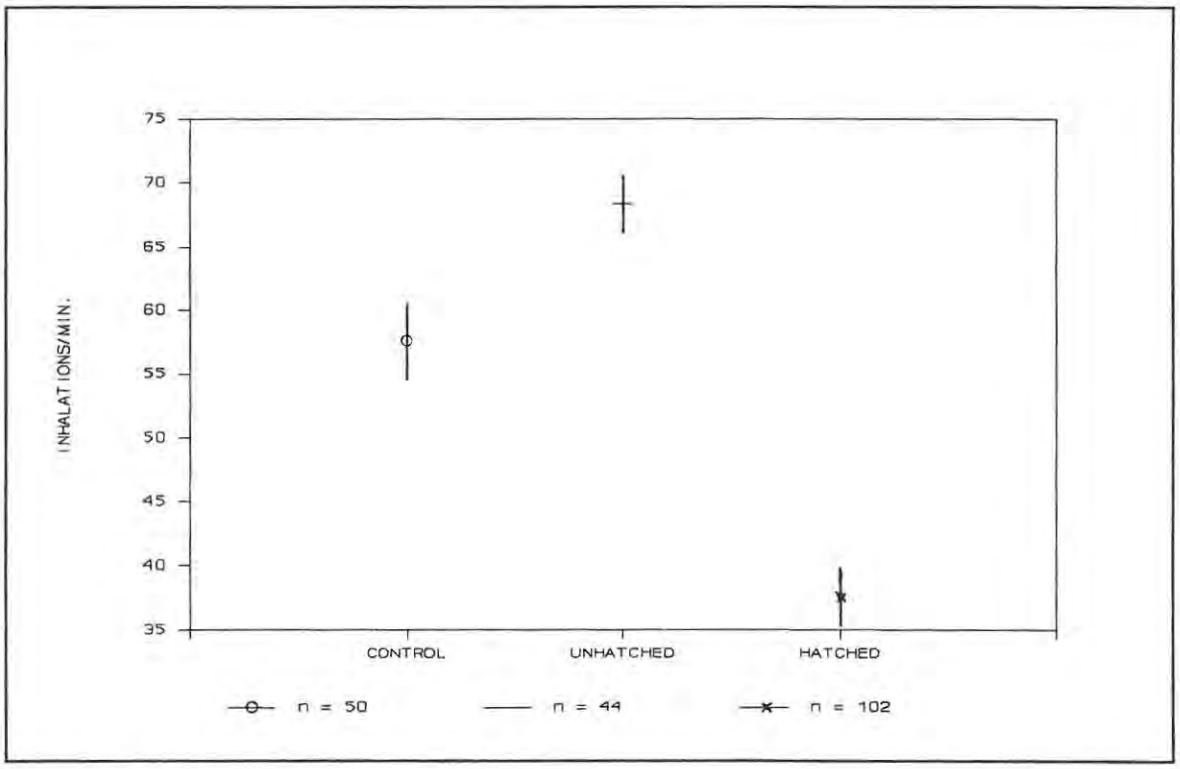


Figure 47. Ventilation rates (inhalations min^{-1}, ± 1 SD) for feeding adults (control), mouth-brooders carrying embryos, and mouth-brooders incubating free-embryos.

The major developmental events describing the stepped continuum in G. feliceps early ontogeny are summarised in Table XV.

Table XV: Summary of the early ontogenetic development of Galeichthys feliceps.

Developmental step	Age (Days:Hrs:Mins)	Important events
Activation $C^1 1$	0:00:00 - 0:19:00	Formation of perivitelline space after 0:12:30.
Cleavage $C^2 2$	0:19:00 - 2:22:00	First cell division at 0:19:00. Morula at 2:22:00. Adhesive membrane sloughs off.
Epiboly & Embryogenesis $C^3 3$	3:00:00 - 10:00:00	Blastodisc and germ ring present after 4 days. Epiboly commenced after7 days and embryogenesis after 9 days. Germ ring $^1/_3$ of the way around yolk.
Organogenesis $E^1 4$	10 - 23 days	First somites after 10 days. Optic vesicles & otocysts after 18 days. Full compliment of somites (45) after 20 days. Cephalic differentiation. Formation of tube-heart & pericardial cavity. 3 prs. rudimentary gill pouches. Epiboly $^3/_4$ complete.
$E^2 5$	24 - 26 days	Left & right lateral vitelline veins after 24 days. First embryo movement - tail lashing and trunk wriggling. Epiboly complete. First red blood cells after 25 days. Dorsal & ventral fin folds. Tube-intestine.
$E^3 6$	27 - 29 days	Prominent eyes & retinal pigmentation. Nasal apertures, rudimentary mouth, maxillary barbel buds, pectoral fin buds. 4 gill arches. Differentiated heart. Vascularised renal plexus. Anterior left & right vitelline veins begin anastomosis. Posterior vitelline plexus expands. Vitelline plexus covers $^1/_2$ yolk surface. Caudal fin fold pointed.
$E^4 7$	30 - 34 days	Anterior & posterior vitelline plexuses linked. Liver developing in association with left lateral vitelline vein. Dorsal flexion of notochord in heterocercal caudal fin. Chondrification of branchial basket. Lapillus otoliths prominent. Gall bladder after 32 days. Sub-intestinal artery prominent and receives blood from caudal vein.
$E^5 8$	35 - 54 days	First ossification in cleithrum. Meckels cartilage prominent. Vitelline plexus completely envelopes yolk. Synchronous mouth and opercular movements. Pectoral, dorsal & caudal fin lepidotrichia after 40 days. Swim bladder present. Stomach differentiation. Gall bladder filled with green bile. First melanophores on head after 43 days. Pelvic fin buds appear. Blood from caudal vein by-passes posterior vitelline vein plexus.
$E^6 9$	55 - 75 days	Paired fin differentiation complete. Dorsal & ventral fin folds well vascularised. Lateral line vesicles on trunk & head. Extensive pigmentation dorsally. 2 gill lamellae. Embryo doubled over with caudal fin covering head region. Posterior vitelline plexus profusely branched.
$F^1 10$	75 - 100 days	Hatching at 75-80 days. Gastro-intestinal differentiation complete. Exogenous feeding commences. Ossification moderately advanced, all skeletal elements partly ossified.
$F^2 11$	100 - 140 days	Period of growth and ossification. Fin folds disappear. Yolk-sac 50% resorbed after 110 days. Yolk-sac 100% resorbed after 130 days. Release of juveniles after 140 days.

Discussion

In a review of reproduction in ariids Rimmer & Merrick (1983) found that the longest recorded incubation period in the literature was nine weeks with the average for six different species being eight weeks. The incubation period for G. feliceps, at between 18 and 21 weeks, is thus considerably longer than those previously recorded for ariids. However, it is apparent from the literature that the above incubation periods were based on estimates rather than experimental evidence. Ward (1957) working on Galeichthys felis (synonymous with Arius felis), found that after artificial fertilisation the two-cell and 16-cell stages of development were reached after four and 11 hours respectively. In G. feliceps these stages were reached after 19 and 29 hours, demonstrating a considerably slower development rate in the cleavage phase. Since most ariids occur in tropical and sub-tropical waters, and since temperature is one of the strongest influences on the rate of development (Blaxter 1969; Kuftina & Novikov 1986), the long incubation period demonstrated by G. feliceps may be a function of its temperate environment.

The advanced stage of development at hatching appears to be peculiar to, and universal amongst, ariids (Gudger 1916, Mansueti & Hardy 1967, Al-Nasiri & Shamsul Hoda 1977, Jones et al. 1978, Rimmer 1985b). However, Balon (1975b, 1977) suggested that in the evolution from substratum guarders to mouth-brooders, earlier hatching was probably induced in the latter in response to two factors, namely the small peri-vitelline space associated with eggs having a large yolk to cytoplasm ratio, and the low oxygen tension of the surrounding water in the buccal cavity.

Evidence generated during the present study would indicate that the above may not be true for G. feliceps. Firstly, the small peri-vitelline space did not appear to inhibit growth since as

the embryo increased in size, so the yolk decreased in volume. While the embryo did appear to be somewhat constricted and cramped close to the time of hatching, when virtually no evidence of a peri-vitelline space remained, the embryo was then at an advanced stage of development. Secondly, it may be argued that the buccal cavity is an oxygen-rich environment. Balon (1981b, p.61) argued that 'some mouth-brooding cichlids, apogonids and probably ariids (Gunter 1947), have their buccal cavities packed to such a degree by the eggs that churning is impossible. The brooding parent respires entirely via the gill apertures'. Under such circumstances the buccal cavity would experience very little flushing at all and would undoubtedly be oxygen-deficient. However, this statement appears to be based on observations of one species of cichlid only (Balon 1977), and certainly does not occur in mouth-brooding G. feliceps, in which ventilation is brought about by the branchial pump mechanism (Fry 1957) in the normal fashion. Observations of mouth-brooding individuals in aquaria demonstrated that embryos situated in the front of the mouth were rocked to-and-fro by a considerable current of inhalant water during breathing movements. Theoretically, water entering the adult buccal cavity would accelerate upon passing over and between the obstructive embryos, much like air does when passing over the upper, curved surface of an aeroplane wing. This phenomenon, together with the increased ventilation rate demonstrated by mouth-brooders in this study, would suggest that the buccal cavity is probably a well-oxygenated environment.

What was apparent from this study, however, was that the ventilation rate of mouth-brooders declined dramatically after hatching of the embryos, indicating that oxygen requirements of embryos were considerably higher than those of free-embryos. The high ventilation rate exhibited before hatching is probably energetically expensive for the mouth-brooder and early hatching should therefore be desirable. As the branchial system is operational, although not yet fully differentiated after

approximately 43 days, it is surprising that hatching does not occur until approximately 75 or 80 days.

More recently Balon (In Press) has argued that in the evolution of mouth-brooding 'Hatching is at first accelerated with the prolongation of brooding time but the larger yolk ultimately facilitates the incorporation of more carotenoid pigments with the ability to provide an endogenous oxygen supply, and so hatching can again be delayed'. This argument is not convincing, however, and in the absence of experimental evidence amounts to mere speculation.

The timing and stage of development at hatching may be influenced by a host of factors. These include the following: the necessity to get rid of accumulating metabolic wastes; the increasing osmoregulatory capabilities associated with organic differentiation; changes in metabolic oxygen requirements at the onset of a new developmental phase; decreased susceptibility to parasite infestation, bacterial or fungal infection; and the need to commence exogenous feeding.

Balon (1985) is of the opinion that hatching is an event of little consequence in ontogeny unless it coincides with the onset of exogenous feeding. In G. feliceps the timing of the onset of exogenous feeding is unknown, although mouth-brooding adults do not appear to pick up detritus or food until several days after hatching has occurred. Free-embryos hatched in incubators will commence feeding immediately if food is available. This would suggest that the digestive system is operational at hatching.

The advanced fin differentiation demonstrated at hatching in G. feliceps is surprising since the free-embryo has no need of them during the extended buccal incubation phase subsequent to hatching. The only manoeuvering ability required is for orientation within the buccal cavity so that the embryo is able to face the inhalant water current. This requirement is

probably universal amongst mouth-brooders in which free-embryos are incubated. Certainly in some cichlids (Balon 1977), hatching occurs when fin differentiation is slight. The advanced fin differentiation at hatching is therefore probably a function of delayed development of some other structures or organs which require the protection afforded by the vitelline membrane.

The development of the vitelline blood plexus differs from that of mouth-brooding cichlids in that the primary vitelline plexus is symmetrical and stems from left and right lateral branches of the paired anterior and posterior cardinal veins. Early in the development the blood is returned to the heart by anterior left and right vitelline veins, which later anastomose to form a single, large anterior vitelline vein leading into the duct of Cuvier, and the heart. In Labeotropheus spp. the vitelline plexus stems from the preanal network of the inferior caudal vein and the sub-intestinal vein and returns to the heart via a single anterior vitelline vein. Later on in the development the hepatic vitelline vein also proliferates on the left-hand side of the yolk, resulting in an asymmetrical vitelline plexus (Balon 1977). The more extensive system found in ariids is probably indicative of the high oxygen and nutrient demand of the very large embryo. Chondrification of the branchial basket commenced after approximately 30 days and blood was seen to flow through the branchial arches for the first time. Gill lamellae appeared after approximately 43 days and coincided with an increased blood flow from the caudal vein into the posterior cardinal vein. This development resulted in a reduction in blood flow to the vitelline plexus and probably marked the onset of combined branchial and vitelline respiration. Strictly speaking, it meant only that oxygenated blood from the vitelline plexus was being diverted through the branchial arches for the first time. It is unlikely that the rudimentary gills would have performed much of an oxygen assimilation function at this time. Considering the small perivitelline space and the consequent restricted volume of

perivitelline fluid, it is indeed unlikely that true branchial respiration occurred before hatching.

The ossification of the skeletal system was considerably delayed and was the last major developmental event to occur. The white substance that appeared in the intestine fairly early in development (after approximately 27 days), increased in size and volume with time and was passed through the vent into the perivitelline space after about 45 days. This substance was deeply stained by Alizarin red, indicating a high calcium phosphate content (Taylor & Van Dyke 1985). It may therefore have constituted an accumulation of excess calcium during the period of development before the onset of ossification. Assuming this hypothesis to be correct, one would expect this calcium to be resorbed at the commencement of ossification, rather than being excreted into the perivitelline space (Plate X). While gas chromatography could be used to reveal the chemical composition of the pellet, acquisition of a sufficiently large sample may prove to be problematic.

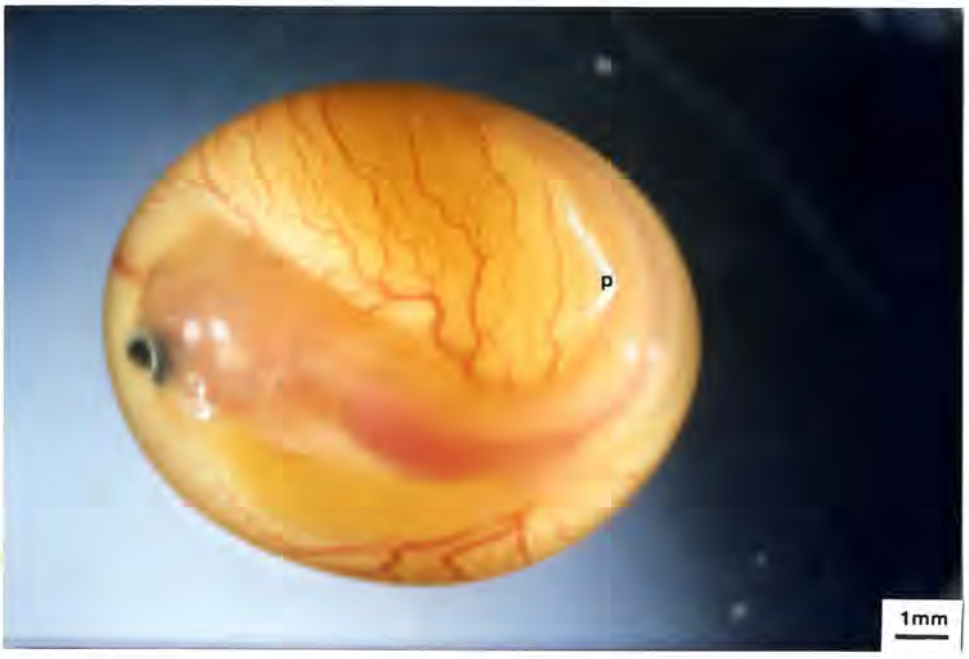


Plate X. Galeichthys feliceps embryo during step $E^{5}8$, demonstrating the nature of the brittle, white pellet (p), excreted into the perivitelline space.

Endogenous nutrition

The yolk of embryonic teleosts is completely enclosed within the syncytium (also known as the periblast) which is situated between, and interfaces with, the yolk on the inside and the vitelline blood capillaries on the outside. All substances derived from the yolk must therefore pass through the syncytium before it can enter the embryonic blood system and be utilised by the embryo (Bachop & Schwartz 1974). Mobilisation of stored energy in the yolk begins with digestion of yolk platelets through the action of hydrolytic enzymes found within the yolk-sac syncytium (Hamlett et al. 1987). The main source for tissue formation in the yolk is protein (Blaxter 1969). In order for it to be utilised by the embryo it must first be converted into amino acids, and then resynthesised into proteins within the embryo. While most of the amino acids would be resynthesised into protein, a certain amount would be needed for energy and would be catabolised. The result of this catabolism is the production of ammonia, which is highly toxic. Smith (1957) found that the egg envelope in salmonids was largely impermeable to the end products of nitrogen metabolism and that these accumulated in the vitelline fluid until hatching. The problem of ammonia toxicity is overcome in many teleosts by breaking it down into a non-toxic form such as urea through enzymatic action in association with the ornithine-urea cycle. Urea may then be stored until hatching (Rice & Stokes 1974). Read (1968 in Blaxter 1969) suggested that the retention of urea served an osmoregulatory function in the early embryos of oviparous and ovoviviparous elasmobranchs. Ariids, which have a high proportion of protein in their yolk and an extensive embryonic period, might be expected to have either an egg envelope permeable to ammonia or the ability to convert and store it as urea.

Duration of the buccal incubation period

It is probable that rates of differentiation and growth within the incubators may have differed considerably from those occurring in the natural environment. In the absence of a

control developmental series (which by definition is an impossibility since the assimilation of such a series would involve at least some manipulation of natural events), they were impossible to detect. However, the project was conducted in order to determine the sequence of ontogenetic events and to elucidate the approximate overall duration of the incubation phase. The former has been accepted as being hierarchical in nature (Maynard Smith 1983 in Greenwood 1989; Balon 1986; Greenwood 1989), and are unlikely to have varied from those occurring in the natural environment, while the latter was more difficult to establish. Although the duration of the oral incubation phase up to hatching (75-80 days) was determined with a reasonable amount of certainty, the period of free-embryo incubation was less certain.

Embryos which were hatched and reared in incubators and fed to satiation each day reached the mean length at release (54mm) at 35 to 45 days after hatching (n = 4 broods). However, they might have grown considerably faster than naturally incubated young, which would probably not have access to as much high protein food. On the other hand, the two aquarium-held mouth-brooders (64-day post-hatching incubation period) might have delayed releasing their young due to the absence of some natural stimulus such as current or a suitable environment in which the young could shelter. The true post-hatching incubation period is therefore likely to fall somewhere between the two extremes of 35 and 64 days. Taking the mid-point would give a total incubation period, from activation to release of juveniles, of approximately 125 to 130 days.

The duration of the mouth-brooding phase in some cichlids has been found to be determined by an innate, internal timing mechanism (Mrowka 1981 in Mrowka 1985), in which free embryos are released after a pre-determined time interval. Aquarium-held mouth-brooders demonstrated that the same mechanism may apply in G. feliceps, although no experimental work has been done to test the hypothesis. Since the young are not released

periodically during incubation as they are in many cichlids, the parent has no visual cue as to the stage of development of its young. However, as their yolk supply becomes depleted, the free embryos are likely to become more demanding in terms of their exogenous food supply. Since it is likely that the source of much of the mucus found in the stomachs of free embryos was the adult buccal cavity itself, the intensity of mucus consumption may also serve as a trigger marking the end of the incubation period.

Saltatory ontogeny or otherwise?

The theory of saltatory ontogeny in fish was originally propounded by Vasnetsov 1953 and Kryzhanovsky et al. 1953 (in Balon 1979), and has subsequently enjoyed considerable mention in the literature (see Balon 1986 for review). However, Greenwood (1989) has recently questioned the validity of the theory and has argued convincingly in favour of an alternative interpretation of ontogeny, namely that of a stepped continuum. Ontogenetic development in a stepped continuum would progress at varying speeds in which the so-called saltations could be likened to periods of accelerated development rather than leaps across discontinuities, as the saltatory ontogeny definition implies. While isolated examples of proposed saltations in the early ontogeny of fish have been presented (e.g. Balon 1979, 1981c; Paine & Balon 1984), they refer mainly to behavioural saltations involving sudden habitudinal shifts of organisms in their environment. While there seems to be little doubt that ontogenetic development is stepped, evidence for saltations (other than behavioural ones), said to occur during thresholds between developmental steps, appears to be lacking. Balon (1981c) has conceded that the identification and verification of saltations would require detailed elaboration of biochemical, physiological, morphological and ethological aspects of ontogeny, information which has yet to be presented in the literature. The writer's opinion is that there is no need to assume, as Balon (1985) does, that saltations are an inherent component of stepped development.

In altricial species particularly, ontogeny is often marked by sudden transitions from one niche to another (Paine & Balon 1984), or by a change from 'jerky to fluent swimming' (Balon 1985). While such behavioural changes are visible, and may indeed be likened to saltations, they are not evident in the ontogenetic development of all species. Cunningham & Balon (1985) studied the early ontogeny in the cyprinodontiform Adinia xenica, in which all of the embryological development occurred within the egg envelope. Although they had difficulty identifying thresholds in the ontogenetic development of this species, the observed ontogeny was nevertheless held to be saltatory. Much of the early ontogenetic development in G. feliceps also occurred within the egg envelope, and while steps were identified on the strength of marked morphological changes, ontogenetic development appeared to be gradual. It should be emphasised that the present study was not conducted in enough detail to test the theory of saltatory ontogeny, although it was evident from this investigation that Balonian ontogenetic saltations are considerably more cryptic than their definition implies.

In conclusion, while artificial fertilisation and incubation was met with limited success, overall ontogenetic development was satisfactorily recorded using several developmentally overlapping broods from wild-caught mouth-brooders. As a result of the slow and apparent gradual ontogenetic differentiation, developmental steps were difficult to identify. Hatching and ossification were considerably delayed and young attained a large proportional body size before being released from the parent buccal cavity. This strategy confers a substantial survival advantage on the young. The prolonged mouth-brooding period has probably been facilitated by the paternal mouth-brooding habit. The ontogenetic characteristics exhibited by G. feliceps are representative of an evolutionarily advanced mouth-brooding strategy.

CHAPTER 5 - AGE AND GROWTH

Introduction

The growth rate of fish is one of the primary biological factors controlling the dynamics of exploited populations (Baranov 1918, Peterson 1903 & Russell 1931 in Beverton & Holt 1957; Ricker 1975; Gulland 1977; Cushing 1981; Everhart & Youngs 1981; Summerfelt 1987). While stock assessment may be performed without age and growth data, using surplus production models (Graham 1935, 1938, Schaeffer 1954, 1957 in Cushing 1981), their inclusion into dynamic pool models (Beverton & Holt 1957), introduces an additional biological element and improves accuracy. Age and growth studies are therefore an important prerequisite for accurate stock assessment.

Several iterative methods are available which mathematically express the growth of fishes (for review see Butterworth et al. 1989), with parameters which may be incorporated directly into stock assessment models. The dynamic pool models, used extensively in fisheries management (Beverton & Holt 1957; Pitcher & Hart 1982), utilise the following age and growth data: age at recruitment; age at sexual maturity; and maximum age reached. Parameters of the growth equation are also used in the determination of asymptotic weight, and natural and total mortality coefficients.

Growth data also form the basis for virtual population analysis (Gulland 1965 in Pope 1983), in which population age structure is used in the determination of annual recruitment and fishing mortality.

The choice of the appropriate method and fitting procedure depends on the nature of the error distribution about the fitted curve (Hughes 1986). Once the error distribution has been modeled using the absolute, relative or transformed

logarithmic model (Hughes op cit.), the most appropriate growth function may be selected. For an error model to be acceptable, the criteria of randomness and homoscedasticity of the residuals must be satisfied. These are statistical tests used to determine the goodness and validity of fit (Punt & Hughes 1989). The growth functions available include the four-parameter Schnute model (Schnute 1981; Schnute 1985 in Hughes & Punt 1988), and several sub-models thereof (Hughes & Punt 1988; Punt & Hughes 1989).

The age composition and growth rate of G. feliceps and G. ater were determined for two reasons. Firstly, to test the predictions of the r- and K-selection theory, namely that K-selected species should exhibit slow growth and longevity. Secondly, to provide the parameters required for the stock assessment models.

Materials and Methods

Preliminary investigation into the use of various hard parts for ageing indicated that the lapillus otoliths were the most suitable structures to use. Other structures investigated were pectoral and dorsal spines, vertebrae, operculae, and sagittal and astericus otoliths. Spine and vertebral sections yielded indistinct growth zones in which it was difficult to identify growth checks. Opercular growth checks were not visible with the naked eye and these structures were rejected.

The lapillae were large, thick and semicircular (Hecht & Hecht 1981), and exhibited relatively distinct growth zones upon sectioning. Fish lengths and lapillus otolith dimensions were positively correlated for both species (Table XVI), indicating that otolith size could be used as a reliable indicator of fish age. In addition, the number of otolith growth rings increased with otolith size, suggesting a relationship between the number of rings and fish age.

Several techniques were initially employed in the attempt to improve the clarity and 'readability' of otolith growth zones. These included:

a) Sectioning - Otoliths were embedded in resin rods and sectioned laterally through the nucleus using a double-bladed diamond-edged saw (Williams & Bedford 1974; Rauck 1976; Beamish 1979).

b) Burning - Whole and sectioned otoliths were exposed to a low heat intensity alcohol flame until browned (Christensen 1964; Hecht & Smale 1986).

c) Staining - Whole otoliths and otolith sections were subjected to ninhydrin staining (Schneppenheim & Freytag 1980).

d) Heating - Whole and sectioned otoliths were heated to 150°C in glycerine (Freytag 1980).

e) Immersion - Whole and sectioned otoliths were immersed and viewed in a variety of liquids including glycerine, methyl salicylate, water and xylene (Williams & Bedford 1974; Hecht & Smale 1986).

f) Polishing - Otolith sections were polished using 1600 grade carborundum paper and 50µm grinding paste (Hecht & Smale 1986).

g) Daily growth rings - Scanning electron microscopy was employed in order to determine the feasibility of using daily growth ring counts in the identification of annuli (Victor & Brothers 1982; Radtke & Targett 1984; Campana & Neilson 1985; Radtke 1987; Pulfrich & Griffiths 1988).

The final procedure adopted for viewing the otoliths was as follows: unburnt otoliths were embedded in a clear polyester resin using metal or plastic moulds. The flexibility of plastic moulds made from longitudinally halved 25mm diameter plastic piping expedited the removal of hardened resin rods. The mould surface was coated with a releasing agent (petroleum jelly, wax-based polish or conventional grease) before embedding. Otoliths were sectioned using a double-bladed diamond edged saw, with sections varying in thickness from 0.35mm to 0.50mm. Otolith sections were fixed onto glass slides using 'D.P.X. Mountant' and viewed under a binocular microscope

between 10X and 30X magnification. The sections were viewed under transmitted light.

While growth zones were visible in whole otoliths it has been shown that in long-lived species, the use of whole otoliths frequently results in age under-estimation (Beamish 1979; Bennett et al. 1982; Beamish & McFarlane 1983, 1987).

Annulus validation

Several methods were used in the attempt to identify annual growth zones.

a) Edge increment analysis was conducted using otolith sections. The month during which the outermost growth zone was at its broadest was identified and the width recorded. The width of the outermost growth zone, in otoliths collected during successive months, was then measured and expressed as a percentage of the maximum observed growth zone width. A plot of the monthly increments revealed whether or not the growth zones were annual.

b) Otoliths from laboratory hatched and reared one year-old G. feliceps juveniles confirmed the presence of a juvenile ring within the nucleus and enabled the identification of the first annulus in otoliths from 'wild' samples.

c) Growth of G. ater juveniles taken in monthly rotenone samples (Smale & Buxton 1989) revealed the size of one year-old fish. The nature of the first annulus in otolith sections could therefore be ascertained.

Reading of otolith sections

Otolith sections were counted three times without reference to size or sex of the animal at intervals of approximately two weeks. Where all three counts differed the section was rejected from the study, while if two out of the three counts were the same a fourth count was made. If after the fourth reading three counts matched, the age was accepted as valid.

The numbers of otolith sections used in the studies were 598 for G. feliceps, of which 53 (9%) were rejected, and 326 for G. ater, of which 22 (7%) were rejected. The sexes were aged separately as length frequency histograms suggested that females of both species grew to a larger size, and were older, than males.

Back-calculation was employed in order to fill sampling gaps for certain age classes. For G. feliceps back-calculated lengths at age for four, five and six year-old fish were included in the growth curve, while for G. ater back-calculated lengths at three, four, five and six years of age were used. Since the relationship between fish length and otolith radius was non-linear, the formula of Ricker & Lagler (1942 in Bagenal & Tesch 1978), was used:

$$Sn = (S\ Sn/S)$$

where Sn = adjusted distance to the nth annulus,
S = average otolith radius for a fish of the observed length,
Sn = radius of annulus 'n',
S = total otolith radius.

The parameter estimates obtained from the adjusted relative error model indicated that either the Schnute (Schnute 1981) or the von Bertalanffy (von Bertalanffy 1934 in Pauly 1981) model could be used to model the growth of G.feliceps males and females, and of G. ater females. An F-test was used in each instance to determine the preferred model (Punt & Hughes 1989). The Schnute model produced the most reasonable fit for G. ater males, and the F-test showed that it was also the preferred model for G. ater females ($F=12.713$; $df=1, 202$). The von Bertalanffy Special model was selected for male ($F=0.0369$; $df=1, 308$) and female ($F=1.73$, $df=1, 329$) G. feliceps.

The von Bertalanffy Special (3-parameters) and Schnute (4-parameters) growth models are described by the following equations:

VON BERTALANFFY SPECIAL

$$l(t) = L_\infty \mid 1 - \exp(-K(t - t_o)) \mid$$

where $l(t)$ = the length at age t,
L_∞ = the theoretical maximum length,
K = growth rate parameter,
t_o = the age at which the fish would commence growing from zero length.

SCHNUTE

$$\ell(t) = \left[\ell_1^{\,b} + (\ell_2^{\,b} - \ell_1^{\,b}) \frac{1 - e^{-a(t - t_1)}}{1 - e^{-a(t_2 - t_1)}} \right]^{1/b}$$

where $l(t)$ = the length at age t,
l_1 = the value of $l(t)$ at time $t=t_1$,
l_2 = the value of $l(t)$ at time $t=t_2$,
a = parameter,
b = parameter.

The observed length-at-age data were processed using 'PC-YIELD' (Hughes & Punt 1988). However, the data failed to meet the requirements for randomness of residuals and homoscedasticity for either the absolute error or the random error models. After additional analysis of the data a successful transformation was obtained (A. Punt Dept. Applied Mathematics, University of Cape Town, pers. comm.), which yielded homoscedastic residuals, using an adjusted relative error model.

The adjusted relative error model used was as follows:

$$l_t = \hat{l}_t \exp (\epsilon_t / a_t^b)$$

where l_t = the length of a fish,
a_t = its age,
$\hat{l}_t$ = the model estimate of the length,
b = a pseudo - parameter,
ϵ_t = a normally distributed error.

Variance estimates of the growth model parameters were determined using the jack-knife re-sampling method (Hughes & Punt 1988).

Since the dynamic pool models generally deal with biomass rather than length data (Beverton & Holt 1957; Gulland 1977, 1978; Cushing 1981; Ricker 1981; Pitcher & Hart 1982), growth in weight was calculated as follows.

For G. feliceps W_∞ was determined from the L_∞ value by substitution in the length-weight relationship, and was then used in the von Bertalanffy equation to calculate growth in weight.

For G. ater mean length at age data were transformed into mean weight at age data using the length-weight relationship.

Results

Nature of the growth zones

The otolith growth zones did not conform to the characteristic hyaline-opaque pattern found in many teleost species native to the South African coast (Botha 1971; Hecht & Baird 1977; Nepgen 1977; Payne 1977; Geldenhuys 1978; Wallace & Schleyer 1979; Coetzee & Baird 1981; Buxton & Clarke 1985; Bennett & Griffiths

1986; Buxton & Clarke 1986; Buxton 1987; Clarke 1988; Griffiths 1988; Pulfrich and Griffiths 1988; Buxton & Clarke 1989). They were composite, comprising two or more indistinct sub-zones of varying opacity, similar to those found by Griffiths & Hecht (1986) and Crozier (1989) for Lophius upsicephalus and L. piscatorius respectively.

The nuclei of both species appeared opaque when viewed under transmitted light. A hyaline check was present within the nucleus. This check may have corresponded to the completion of yolk absorption and the onset of exogenous feeding (Dmitrenko 1975), (Plates XIa & b).

The hyaline checks between successive growth zones were generally more distinct than those occurring within the growth zones (Plate XIIa). After sexual maturation, the growth zones became narrow and less easily distinguishable (Plate XIIb).

In otoliths from older fish counts were best made along the medial edge of the section where growth zones were narrow and growth checks most easily defined.

Annulus validation

Edge increment analysis using otolith sections revealed that in G. feliceps the annual growth zone commenced in September and reached maximum width in August of the following year. The analyses were determined for otolith sections with three and four growth zones. In G. ater growth zones commenced in August and were complete by July of the following year. Fish with between five and nine growth zones were used in the analyses (Figs. 48 & 49). The analyses revealed that the growth zones represented annuli.

Plate XIa. Otolith section from a 1^{+}-year old G. feliceps juvenile: n=nucleus, j=juvenile ring, x=annulus.

Plate XIb. Otolith section from a 1^{+}-year old G. ater juvenile demonstrating the nature of the annulus: n=nucleus, j=juvenile ring, x=annulus.

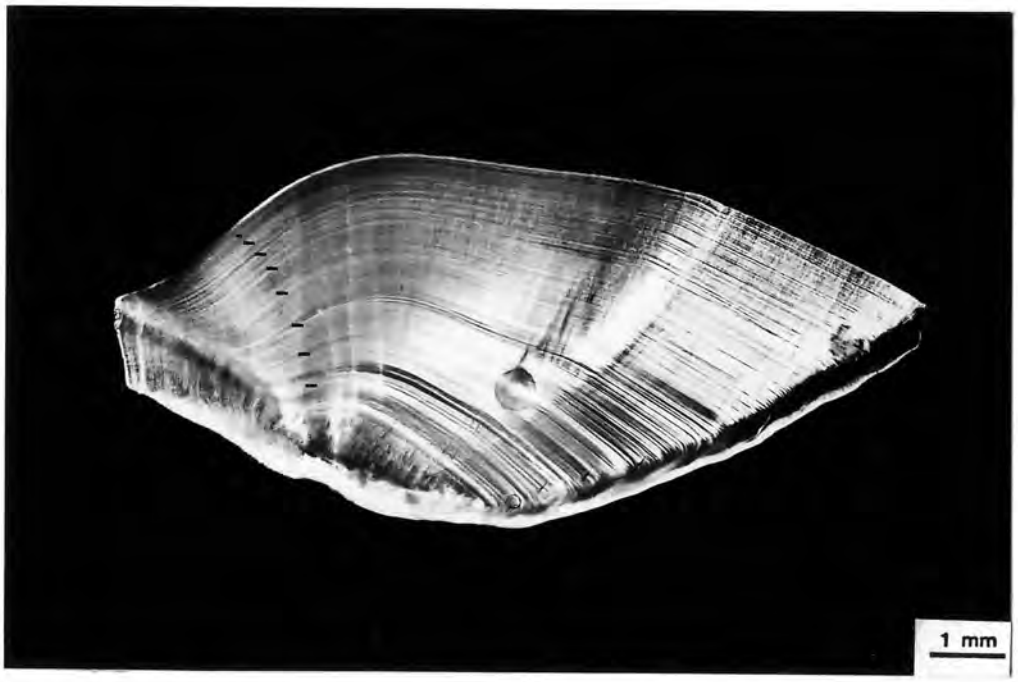


Plate XIIa. Otolith section from an 8-year old G. feliceps female demonstrating the nature of the annuli (-).

Table XIIb. Otolith section from a 15-year old G. ater male demonstrating the deterioration in annulus structure towards the otolith edge: - =annuli.

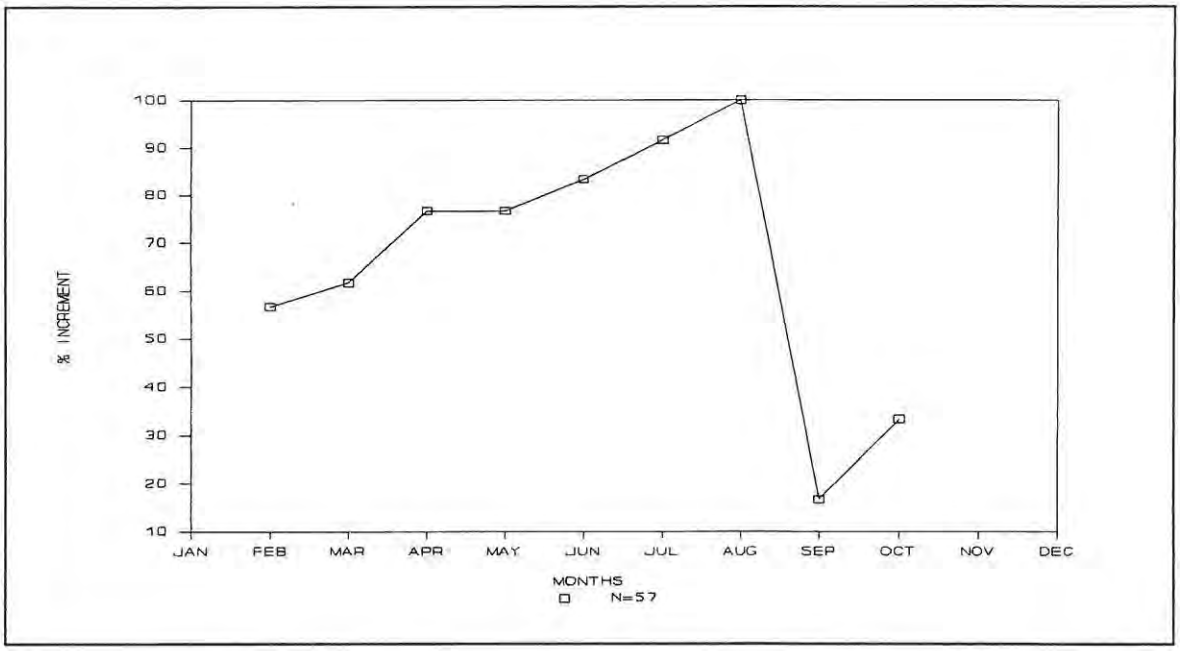


Figure 48. Monthly edge increment analysis in G. feliceps using otolith sections from fish aged at three and four years.

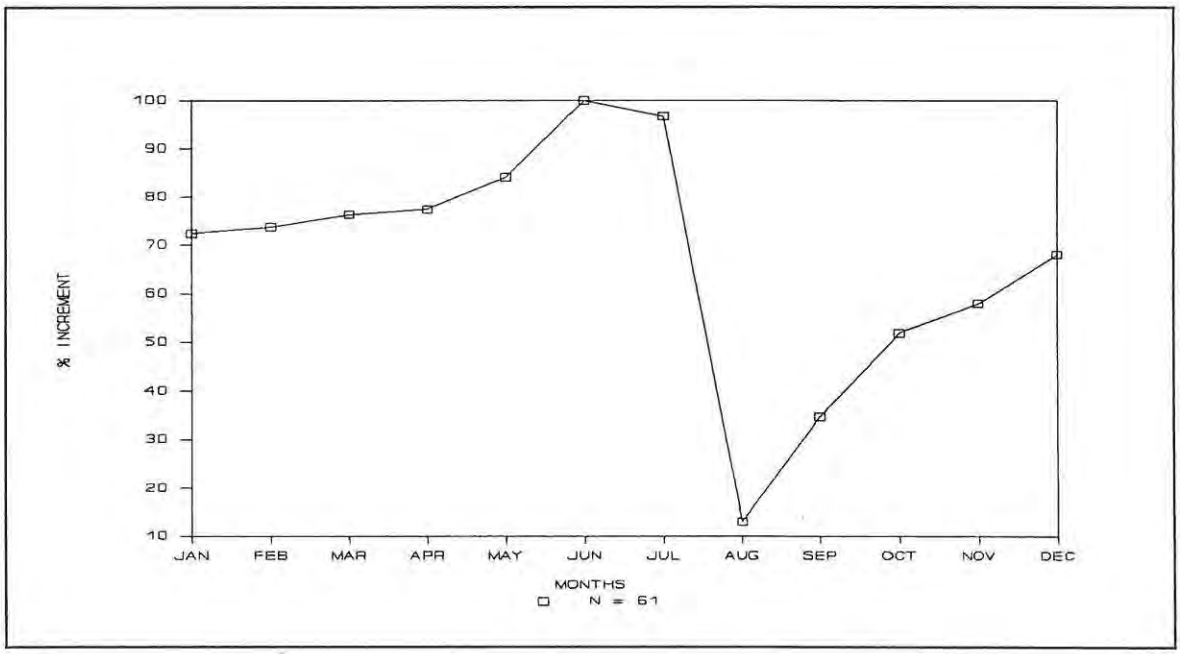


Figure 49. Monthly edge increment analysis in G. ater using otolith sections from fish aged at between five and nine years.

Known age G. feliceps hatched and reared in aquaria over a two-year period were used to confirm early growth rates (Fig. 50). Similarly, growth rates of young-of-the-year G. ater obtained from monthly rotenone samples were used to confirm the size of one year-old fish, as established from otoliths (Fig. 51). This information enabled the identification of the first annulus and confirmed the presence of a juvenile ring.

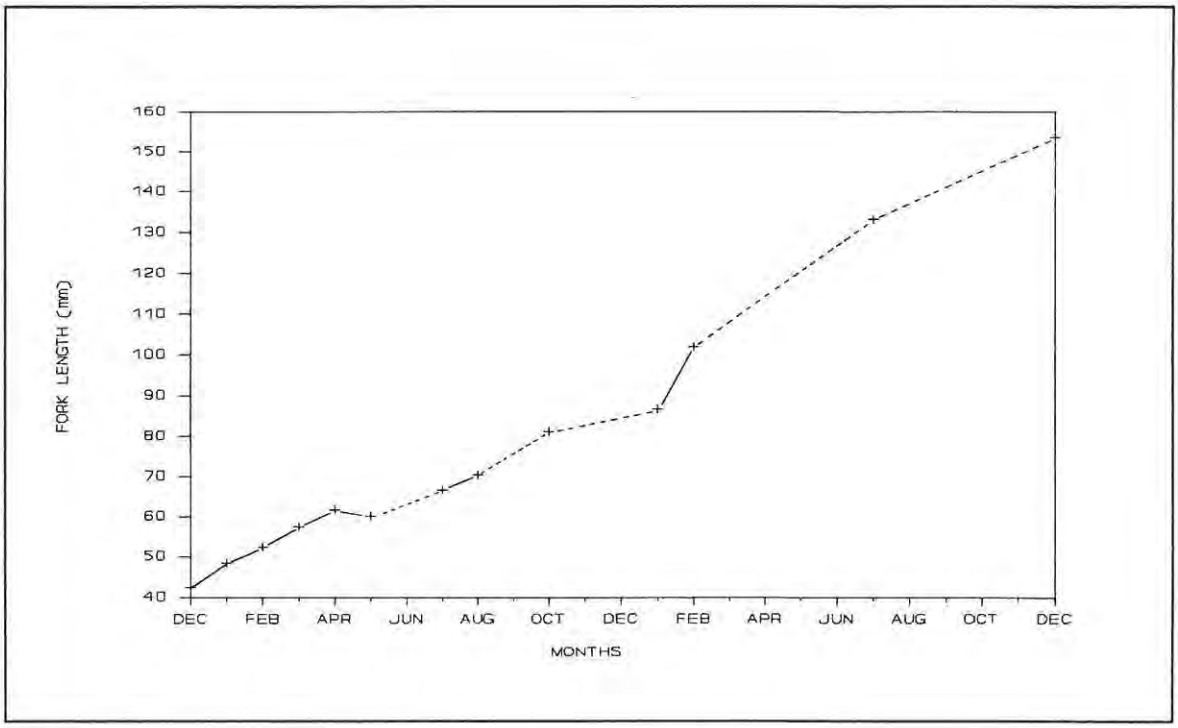


Figure 50. Growth of laboratory hatched and reared G. feliceps juveniles. As spawning occurred in September, the curve illustrates that lengths (FL) of approximately 75 and 145mm were attained after 12 and 24 months respectively.

G. feliceps males and females were aged to 16 and 18 years respectively. Difficulty was experienced with the interpretation of growth zones near the edge in some of the larger otoliths. Since these sections were rejected from the study, both species may have been under-aged by between three and five years.

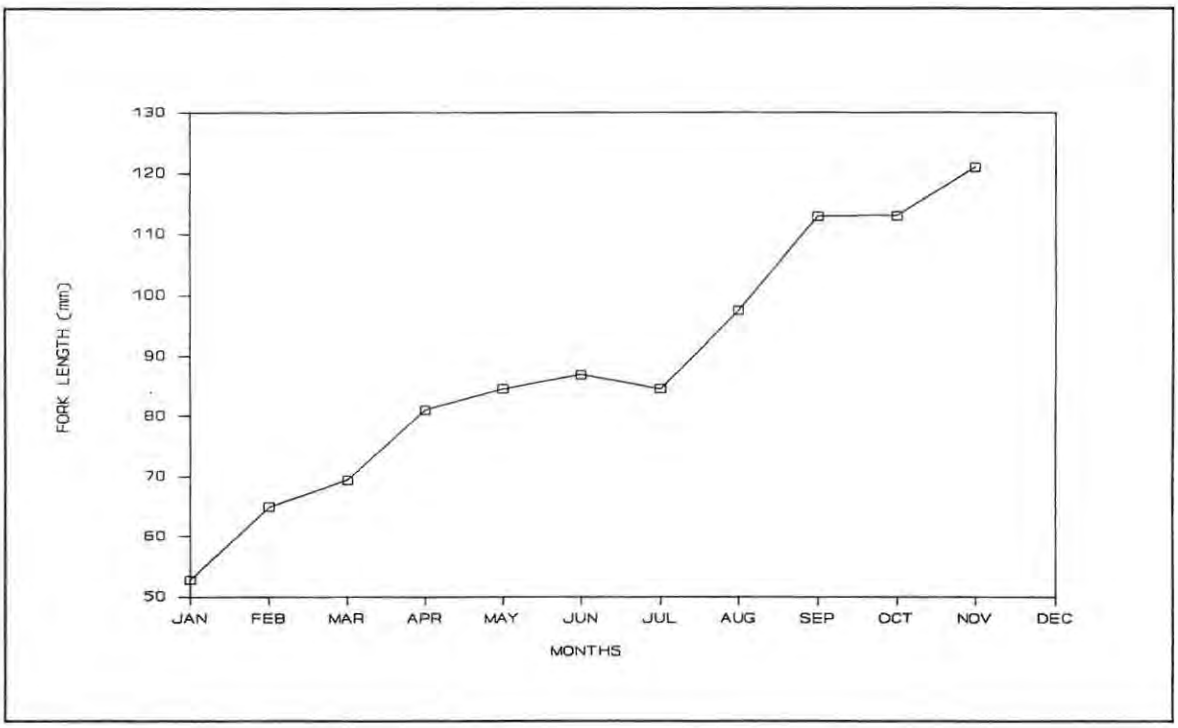


Figure 51. Growth of G. ater juveniles caught in monthly rotenone samples. Since spawning occurred in August, the curve illustrates that a length (FL) of approximately 95mm was attained after one year.

G. ater males and females were aged up to 15 years although some otoliths which may have been up to 18 years of age were rejected on the strength that three successive counts did not concur. Clarity of growth zones also tended to deteriorate near the otolith edge in many of the older specimens, precluding accurate interpretation.

There were no significant differences between the sexes in the relationships between fork length and otolith radius, otolith length or body mass (t-test, $p<0.05$), for either species (Appendix IIa). The regression equations for the relationships between fork length and otolith length, otolith radius and body mass are presented in Table XVI and the parameters of the growth models in Table XVII.

Table XVI: Relationships between fork length and otolith length, otolith radius and body mass for G. feliceps and G. ater.

REGRESSION:	G. FELICEPS	G. ATER
FL vs OR:	FL = 45.27xOR^1.18 (r^2=0.979)	FL = 51.58xOR^1.01 (r^2=0.953)
FL vs OL:	FL = 17.19xOL^1.19 (r^2=0.983)	FL = 16.91xOL^1.14 (r^2=0.981)
FL vs Wt:	Wt=9.55E-06xFL^3.08 (r^2=0.998)	Wt=1.38E-05xFL^3.04 (r^2=0.999)

Table XVII: Parameters and standard errors of the von Bertalanffy and Schnute growth models for G. feliceps and G. ater respectively.

MALES	(S.E.)	FEMALES	(S.E.)
		G. FELICEPS	
L_∞ = 389.895	(15.182)	L_∞ = 407.847	(5.490)
t_0 = -1.406	(0.227)	t_0 = -1.834	(0.0894)
K = 0.147	(0.017)	K = 0.119	(0.00502)
		G. ATER	
a = 0.274	(0.00549)	a = 0.0739	(0.0448)
b = 1.072	(0.00575)	b = 2.265	(0.569)
l_1 = 69.289	(1.532)	l_1 = 46.3	(104.221)
l_2 = 358.176	(0.801)	l_2 = 292.62	(2.450)
L_∞ = 279.344	(1.221)	L_∞ = 348.407	(39.693)
t_0 = N/A		t_0 = -0.141	(0.364)
K = 0.274	(0.00549)	K = 0.074	(0.0448)

The age-length keys for the two species are presented in Tables XVIII, XIX, XX & XXI.

The mean observed lengths at age between the sexes in G. feliceps were not significantly different. In G. ater the older

age classes were significantly different in size ($P<0.05$), with females being the larger sex (Appendix IIb). However, the growth curves for the sexes were found to be significantly different in both species (G. feliceps $F=30.492$; $df=4, 641$: G. ater $F=19.218$; $df=4, 412$), and were therefore plotted separately. The growth curves for males and females of both species are shown in Figures 52, 53, 54 & 55. Mean observed fork lengths (± 1 SD), are plotted together with the modeled curves.

Back-calculation was conducted for ages 0 - 9 only since the annuli after sexual maturity were not validated. Student's t-test showed no significant differences in the back-calculated lengths at age between the sexes of either species ($P< 0.05$) (Appendix IIc).

Student's t-tests of mean observed vs. back-calculated lengths at age yielded significant differences for 7, 8 & 9 year-old G. feliceps, suggesting the presence of Rosa Lee's phenomenon (Bagenal 1978). The observed and back-calculated values are presented in Table XXII.

Growth in weight for G. feliceps was described using the von Bertalanffy growth model as follows.

$$\text{Males: } w(t) = 928.74\ |1 - \exp(-0.16(t + 2.35)\ |^{3.083}$$

$$\text{Females: } w(t) = 1064.16\ |1 - \exp(-0.16(t + 1.85)\ |^{3.083}$$

For G. ater mean weight at age data were used to construct the curve. Growth in weight is graphically presented in Figures 56 & 57.

Table XVIII: Age-length key for G. feliceps males. Fork lengths in mm. are used throughout.

SIZE CLASS	AGE																		ALL AGES
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
40-59	16																			16
60-79	14																			14
80-99	4	1																		5
100-119		13																		13
120-139		7	3																	10
140-159			19																	19
160-179			14	10																24
180-199				10	3	1														14
200-219					5	3														8
220-239					4	5	2													11
240-259						4	8	1												13
260-279						1	10	3	3											17
280-299							1	9	7	6	3									26
300-319									9	13	11	2	2							37
320-339										11	18	13	10	6	3					61
340-359												1	2	2		4	8			17
360-379																	1			1
ALL SIZES	34	21	36	20	12	14	21	13	19	30	32	16	14	8	3	4	9			306

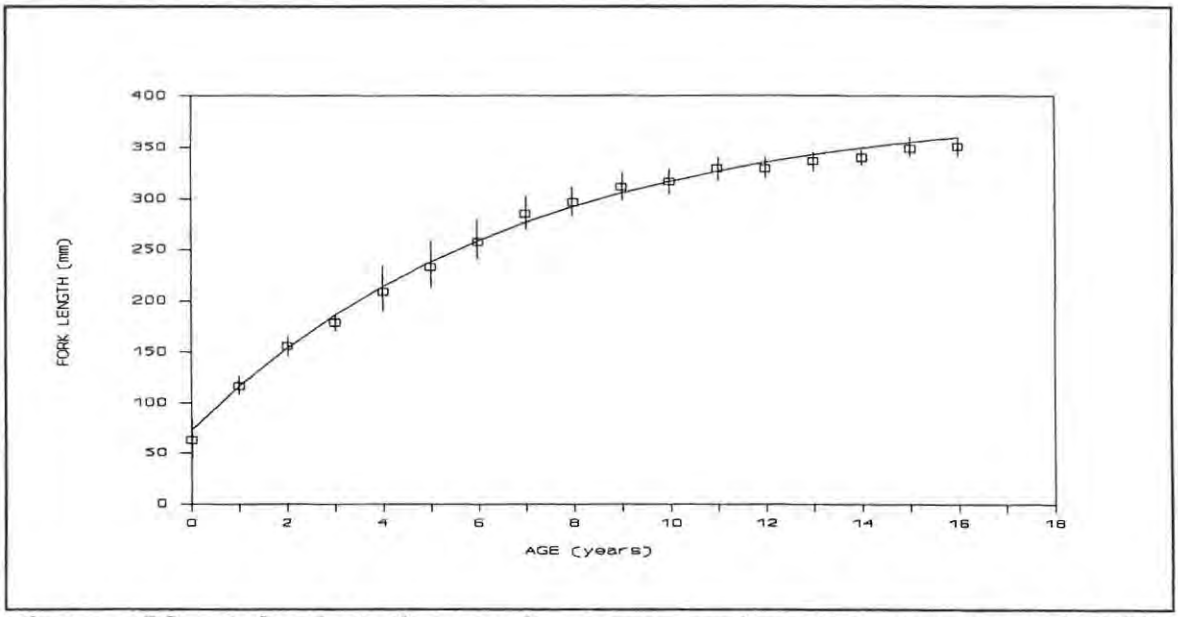


Figure 52. Calculated growth curve (using the von Bertalanffy Special model) and mean observed lengths at age (±1 SD), for G. feliceps males.

Table XIX: Age-length key for G. feliceps females.

SIZE CLASS	AGE																		ALL AGES
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
40-59	16																			16
60-79	14																			14
80-99	4	1																		5
100-119		12																		12
120-139		7	2																	9
140-159			21	1																22
160-179			11	11	2															24
180-199				13	10															23
200-219					6	9	4													19
220-239					1	6	8													15
240-259						1	4	4												9
260-279							6	4	2											12
280-299							1	2	6	6		2								17
300-319									6	13	6	4	7	1						37
320-339										8	13	6	9	14	3					53
340-359												4	3	5	6	9	8	1		36
360-379																		6	1	7
ALL SIZES	34	21	34	25	19	16	23	10	14	27	19	16	19	20	9	9	8	7	1	330

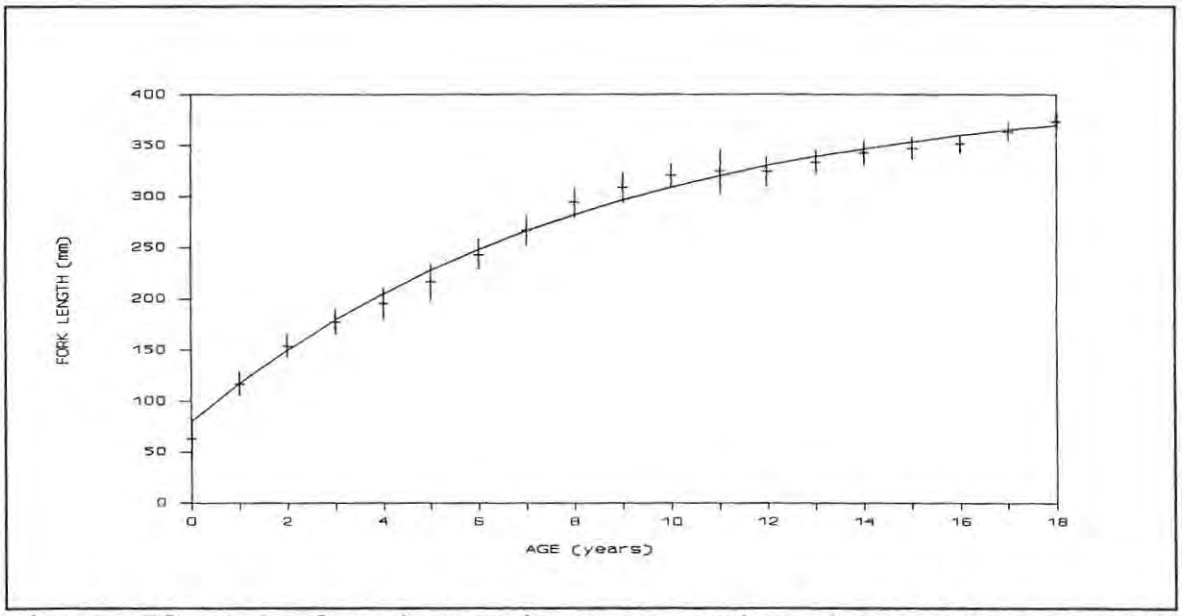


Figure 53. Calculated growth curve (using the von Bertalanffy Special model) and mean observed lengths at age (± 1 SD), for G. feliceps females.

Table XX: Age-length key for G. ater males.

SIZE CLASS	AGE															ALL AGES
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
60-79	7																7
80-99	11																11
100-119		6	2														8
120-139		1	5	1													7
140-159			7	4	1												12
160-179			1	6	4	1											12
180-199				4	6	6											16
200-219					4	7	5										16
220-239							5	4		1							10
240-259								12	18	18	15	5	1				69
260-279									1	4	8	8	9	5	2	1	38
280-299															1	5	6
300-319																	
ALL SIZES	18	7	15	15	15	14	10	16	19	23	23	13	10	5	3	6	212

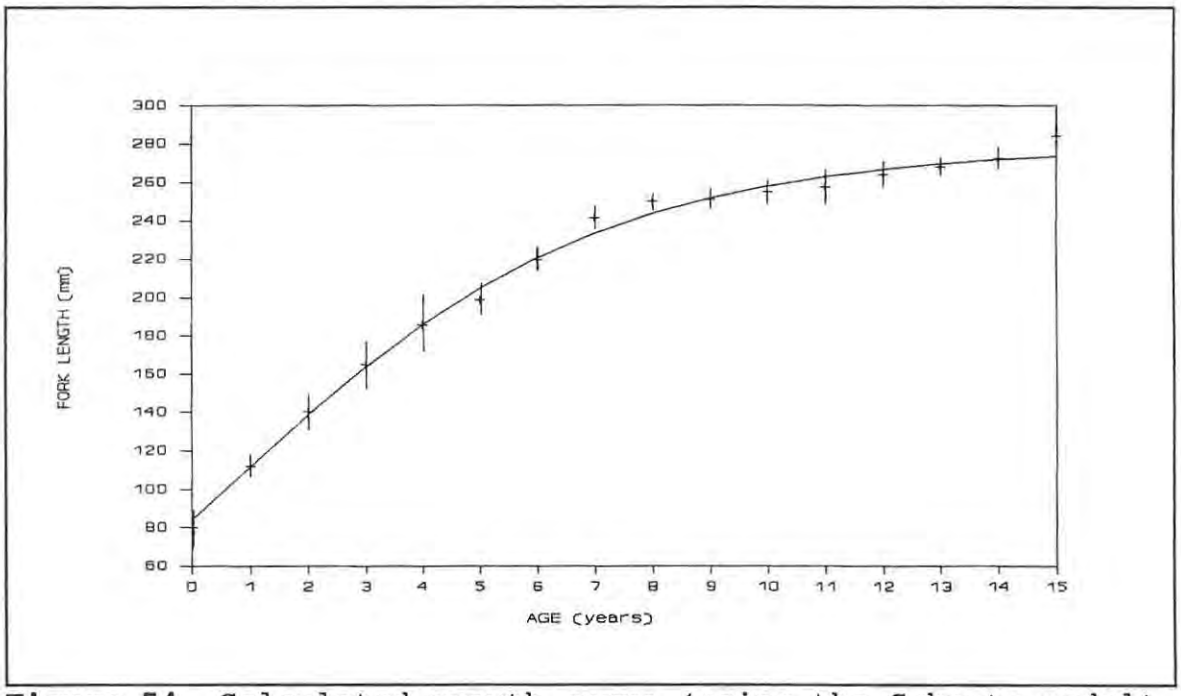


Figure 54. Calculated growth curve (using the Schnute model), and mean observed lengths at age (± 1 SD), for G. ater males.

Table XXI: Age-length key for G. ater females.

SIZE CLASS	AGE																ALL AGES
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
60-79	7																7
80-99	11																11
100-119		6															6
120-139		1	3														4
140-159			5	1													6
160-179			3	2													5
180-199				3	3	2											8
200-219					3	8	3										14
220-239						4	3	3	2								12
240-259								1	8	9	3						21
260-279									2	2	9	7	15	15	1		51
280-299													10	9	24	11	54
300-319														2	1	1	4
ALL SIZES	18	7	11	6	6	14	6	4	12	11	12	7	25	26	26	12	203

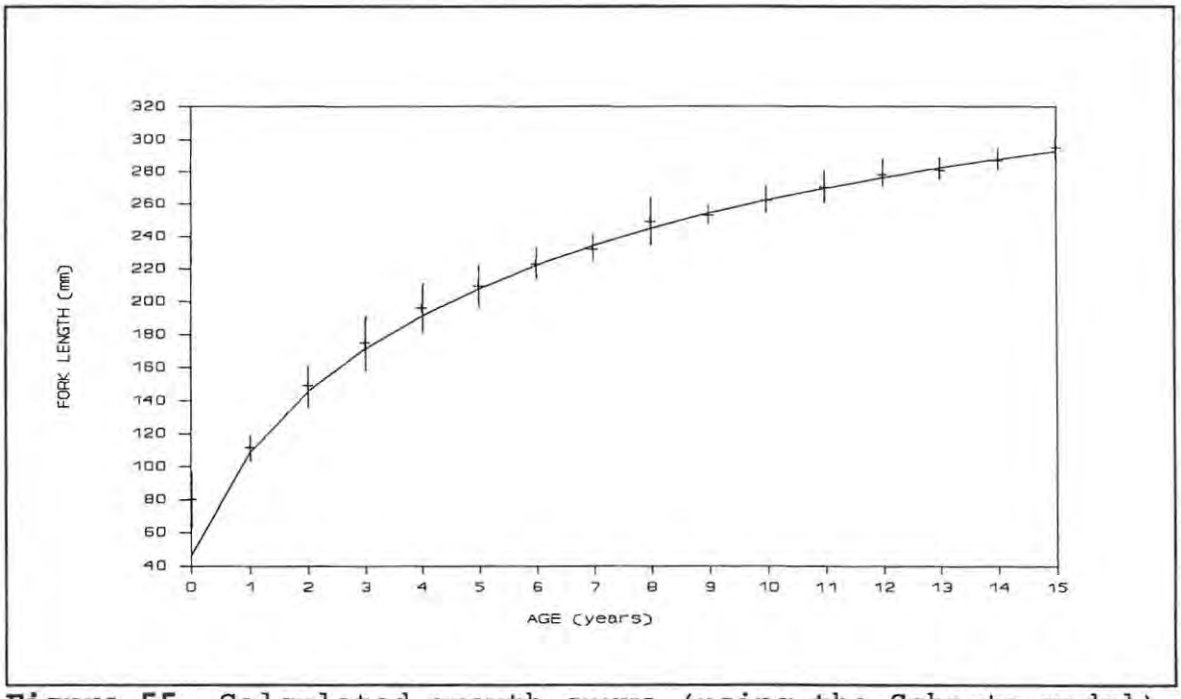


Figure 55. Calculated growth curve (using the Schnute model), and mean observed lengths at age (± 1 SD), for G. ater females.

Table XXII: Tests for significant differences between mean observed and back-calculated fork lengths at age in G. feliceps and G. ater.

AGE	N	MEAN FL (OBSERVED)	SD	N	MEAN FL (BACK-CALC)	SD	T-TEST	SIG DIF (*)
				G. FELICEPS				
0	34	63.1	14.86	27	80.3	9.74	-2.7123	*
1	20	116.9	11.08	27	117.5	15.73	-0.0759	
2	36	155	9.42	27	151	17.74	0.5785	
3	45	178.1	8.87	27	179.1	18.38	-0.1507	
4	32	200.4	16.73	27	203.3	16.63	-0.3327	
5	31	224.7	18.14	27	224.2	14.56	0.0581	
6	45	250.2	19.45	27	241.9	13.84	1.0242	
7	26	278.2	17.53	27	257.8	14.38	2.3267	*
8	33	295.5	12.6	26	273.4	14.2	3.1447	*
9	57	310.5	11.7	25	286.5	14.98	3.7499	*
				G. ATER				
0	18	80.3	10.98	25	83.8	9.07	-0.5647	
1	7	111.9	6.67	25	116.9	9.61	-0.7182	
2	15	144	14.56	25	144.9	12.3	-0.1026	
3	23	168.6	15.01	25	169.2	13.19	-0.0736	
4	22	189.1	15.35	25	188.9	13.58	0.0236	
5	28	204.3	13.39	24	206.8	13.36	-0.3360	
6	16	221	9.61	21	218.7	10.26	0.3488	
7	20	239.6	9.32	19	231.2	8.96	1.4344	
8	30	249.6	7.23	15	242.1	9.44	1.4227	

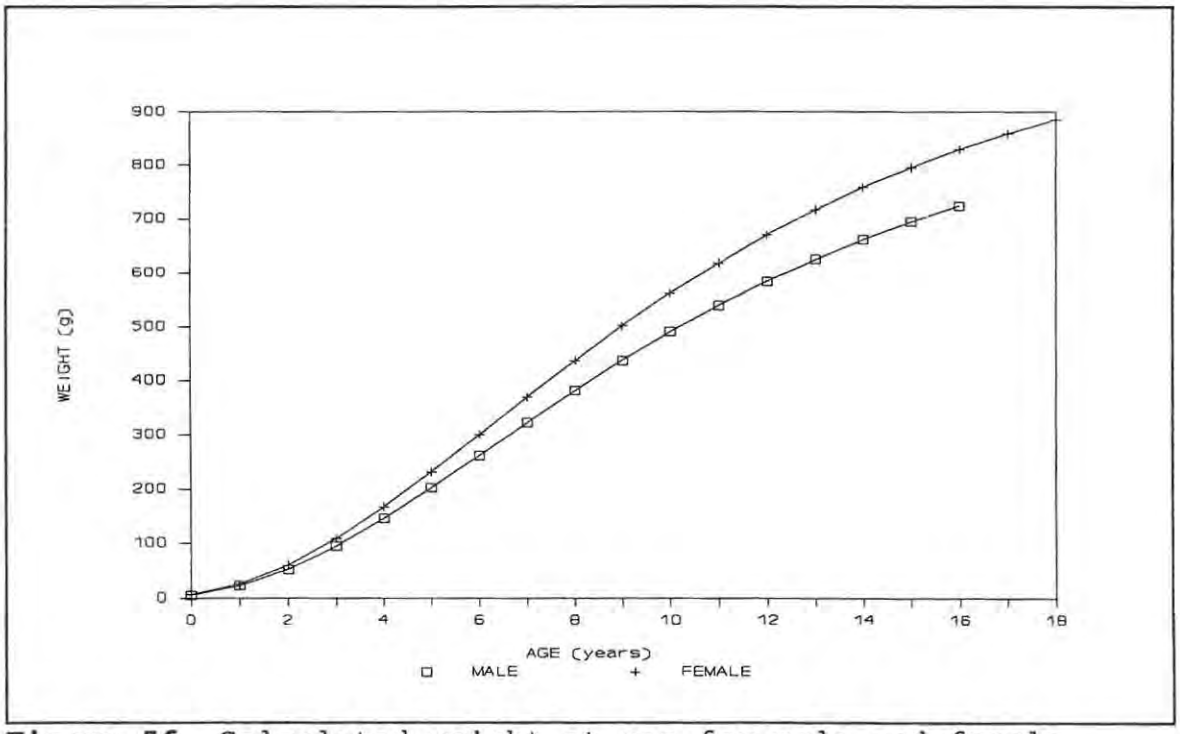


Figure 56. Calculated weight at age for male and female G. feliceps.

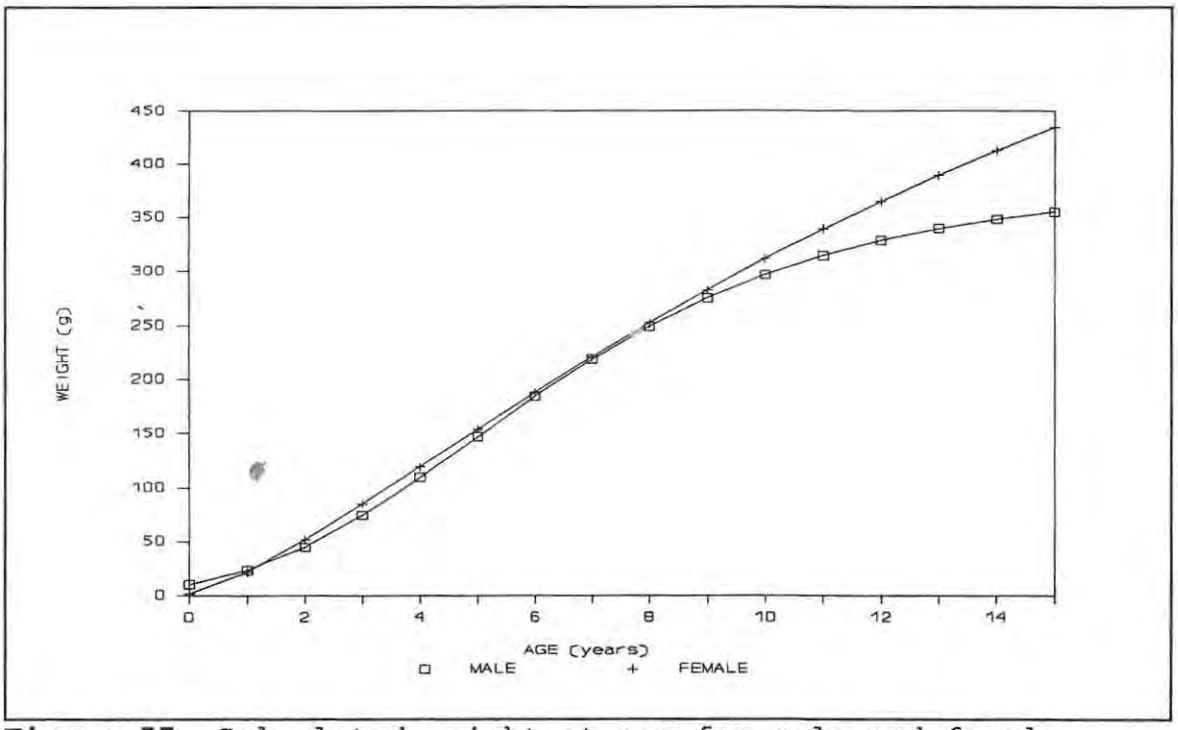


Figure 57. Calculated weight at age for male and female G. ater.

Discussion

While the largest G. feliceps aged in this study compare reasonably well with the maximum sizes recorded in the literature it is apparent that for G. ater this was not the case. The largest G. ater individuals sampled in the study were considerably smaller than maximum sizes recorded for the species. The largest specimens of both species obtained in samples off Port Alfred were a 435mm (TL) female G. feliceps and a 350mm (TL) female G. ater. Castelnau (1861) reported that G. feliceps and G. ater reached total lengths of approximately 45cm and 55cm respectively in Cape waters. Taylor (1986), on the other hand, mentions maximum sizes of 55cm and 45cm for G. feliceps and G. ater respectively, although the length of an illustrated G. ater presented is given at 48cm (Taylor op cit.). The modal size for G. ater in the Port Alfred population was considerably smaller than that of G. feliceps (± 310mm vs. ± 370mm, [TL]). However, a single preserved G. ater specimen

found in the JLB Smith Institute collection (sampled off Cape Point in 1975), was found to be 40cm (TL), which is considerably larger than that of the largest G. ater specimen sampled in the Port Alfred area. Follow-up sampling in the Cape Point area will have to be done in order to establish whether the species does indeed grow to a larger size there, and if so, whether this is the result of faster growth or longevity.

Ariid age and growth studies in the literature yielded results which varied considerably with respect to both growth rate and longevity (Table XXIII).

Table XXIII: Comparative ariid age and growth data from the literature.

SPECIES & AGEING METHOD	MAXIMUM AGE	REFERENCE
Pectoral fin ray section:		
Arius couma	5	Meunier et al. (1985)
A. proops	3.5	Meunier et al. (1985)
A. proops	3	Lecomte et al. (1986)
Whole otolith & Whole operculum:		
Tachysurus tenuispinis	3.5	Dan (1980)
Whole otolith:		
Bagre bagre	6	Costa & Juras (1981/82)
G. caerulescens	6	Warburton (1978)
Otolith section:		
A. thalassinus	9-11	Dmitrenko (1975)
A. thalassinus	19	Bawazeer (1987)
Galeichthys ater	15	This study
G. feliceps	18	This study
Netuma barba	36	Reis (1986b)
Whole vertebrae & Length frequency:		
T. sona	6	Singh & Rege (1968)
Length frequency:		
Ariopsis bonillai	52	Cortés (1984)

Since all known ariids are mouth-brooders (Rimmer & Merrick 1983) with a low fecundity, a characteristic of K-selected fish (Adams 1980), they might generally be expected to exhibit other K-selected characteristics such as slow growth and longevity. The wide range of maximum observed ages (3.5 - 53 years) exhibited in ariid age and growth studies is therefore unexpected. Noticeably, studies using whole otoliths, operculae and vertebrae resulted in consistently lower ages being obtained than those in which otolith sections were used. This may indicate that age was under-estimated in the former studies, rather than it being over-estimated in the latter.

Certainly for Arius proops and A. couma (Meunier et al. 1985), maximum observed sizes of approximately 72 and 80 cm (SL) at ages 3.5 and 5 years respectively, suggest growth rates equivalent to those of many extremely fast growing pisciverous (game-fish) species (Van der Elst 1981). Considering the ariid diet (omnivory) and K-selected life-history characteristics, such rapid growth rates are highly unlikely for this family.

In order to compare results obtained using whole versus sectioned otoliths, the method of Warburton (1978), an otolith check technique using whole otoliths, was tested in the present study. It was found that many growth checks were obscured in older whole otoliths due to a stacking effect near the growing edge, a phenomenon that has been recorded in otoliths from several species (Blacker 1974; Clarke 1988). These checks were elucidated only upon viewing otolith sections. Bennet et al. (1982) were confronted with this phenomenon while ageing the scorpaenid Sebastes diplora, in which whole and sectioned otoliths yielded markedly different counts. Using radiometric analysis, in which the magnitude of the $^{210}Pb/^{226}Ra$ disequilibrium was determined as a function of otolith weight, they were able to show that the counting of growth zones in sections provided the best estimate of fish age, and that counts using whole otoliths lead to under-estimation in older fish.

While the cessation of feeding during mouth-brooding by adult males may have affected growth, this was not manifest in the pattern of growth ring deposition, as there was no apparent difference in appearance between mature male and female otolith sections. The continued growth of otoliths during periods of starvation has been documented by several authors (see review in Campana & Neilson 1985), and it has been found that although mean increment width decreases during starvation, the extent with which starvation influences increment width appears to be related to metabolic rate. Increments were found to be affected to a greater extent in animals with higher metabolic rates (Campana 1983a in Campana & Neilson 1985). This may explain the similarity in annulus appearance and size between males and females in Galeichthys, since sexual maturation occurs at an advanced age when metabolic rate is likely to have slowed considerably. Otolith increment deposition is under the control of an endogenous circadian rhythm, which operates regardless of starvation (Campana & Neilson op cit.).

The use of fluctuations in hepatosomatic indices (HSI) is a good indicator of short-term changes in growth rate (Adams & McLean 1985). Other indices such as relative condition factors and visceral fat-somatic indices (FSI) are less sensitive to short term changes and respond better to long term changes such as those occurring annually. This had direct bearing on male G. feliceps which showed dramatic fluctuations in both HSI and FSI during mouth-brooding. The growth rates of males is likely to decrease during the mouth-brooding period whereas females, which do not show a marked fluctuation in HSI or FSI, might be expected to maintain a normal growth rate.

Strictly speaking, the presence of Rosa Lee's phenomenon in the data for G. feliceps should have precluded the use of back-calculated lengths in the modeling process. However, since data was missing for four year-classes (3, 4, 5 & 6 year-old fish), the use of the back-calculated lengths at age was considered preferable to modeling their growth with missing year-classes.

The missing year-classes may have been due to their inaccessibility to fishermen. For example, the zone just behind the breaker line where they may well occur, is largely out of reach to both the shore angler and the boat fisherman.

The observation that Rosa Lee's phenomenon was present in the data might, however, have been an artefact. Since the species is slow growing, resulting in very little difference in size between the successive age classes, it is unlikely that selective natural or fishing mortality would have occurred, i.e. that there would have been greater survival of the smaller sized fish of a given age group. In addition, the back-calculated data were derived from a sub-sample of otoliths (Males, n=11; Females, n=16) rather than from the entire sample (n=645).

For back-calculation to be used with confidence, two criteria have to be satisfied. A good correlation should exist between otolith dimension and fish length, and measurement of annulus radius should occur between the nucleus centre and some consistent point along the annulus edge. During sectioning of otoliths even slight variations from the centre of the nucleus can lead to fairly substantial errors in subsequent measurements of annulus radii. Errors also arise as a result of the three-dimensional nature of otolith sections, the third dimension being the thickness of the section. When an otolith section is cut too thick, a different set of measurements would arise depending on which of the two lateral surfaces was used.

Bartlett et al. (1984) emphasised the importance of obtaining the best possible relationship between fish length and indicator (otolith) size. They found that the traditionally used regression techniques which generally yield significant relationships can be improved using analysis of covariance. Using ANOVA, in which the relationship between fish length and otolith size is determined separately for each age class, the accuracy of back-calculated data can also be improved.

The growth curves indicated that both species were slow growing and late maturing, a predicted trend in K-selected fish (Adams 1980). Ages at 50% sexual maturity for G. feliceps males and females were 9 and 8 years, and for G. ater, 8 and 7 years respectively, a result which suggested that these species might be particularly vulnerable to recruitment over-fishing.

In G. feliceps a difference in average body mass between the sexes was apparent at an early age, with females being the heavier sex. The disparity in weight increased with age and males tended toward asymptotic growth soon after sexual maturity. In G. ater it was also evident that the onset of sexual maturity in males lead to a leveling off of growth at an earlier age than it did in females.

Age determination using otoliths invariably involves a level of subjective decision making (Brothers 1987), and the reliability of age and growth studies depends largely on factors such as the experience of the investigator, familiarity with the life history style of the species under study and an understanding of the relationship between the biology of the animal and the physiological processes of organic and inorganic material deposition within the otolith. As stated by Sych (1974), interpretation should precede counting. He equated ageing of fish to telecommunication, in which the recorded information stored within the black box/structure being used (the age of the fish) needed to be decoded before it could be received/understood by the addressee/reader. In addition, he stated that the information encoded on the structure assumed different forms depending on the nature of the fish population and the conditions to which it had been exposed. He emphasised the importance of setting up, and adhering to, a decision rule which relates to the investigator's concept of annual rings as distinguished from non-annual rings, and which takes into account the spawning season and any other important environmental events. He provided a technique for testing the effectiveness of a formulated decision rule, but conceded that

the only way of verifying a decision rule was to compare the results with a sample of otoliths from known age fish. However, Beamish & McFarlane (1983) have shown that other verification techniques such as mark and recapture, edge increment analysis and cohort analysis may be equally effective in the absence of known-age reference samples.

In the present study, annulus structure was confidently established up to the age at sexual maturity for both species. Beyond this age the structure changed and became increasingly difficult to interpret. It is therefore acknowledged that for large fish ages may have been either over or under estimated. While mark and recapture studies were attempted using oxytetracycline injection of sexually mature animals (Wild & Foreman 1980; Leaman & Nagtegaal 1987), none of these were recaptured. The data is therefore used with constraint until such time as all annuli have been validated.

In conclusion, the rejection of a small proportion of the larger otolith sections from the study due to poor readability may have resulted in an incomplete representation of age classes for both species. The results demonstrated that G. feliceps and G. ater are slow growing and long-lived. Females tend to live longer and exhibit faster growth in terms of weight (both species) and length (G. ater) after the age at sexual maturity.

For management purposes the vital information required was knowledge of the age at recruitment into the fishery and age at sexual maturity, both of which can be successfully determined using the established growth curves.

CHAPTER 6 - POPULATION DYNAMICS

Introduction

The Port Alfred fishery dates back to the early 1900's when several sparid species such as Roman Chrysoblephus laticeps, dageraad C. cristiceps, red stumpnose C. gibbiceps and poenskop Cymatoceps nasutus formed the bulk of the catch. By the mid-1960's, however, they had become rare and effort was largely redirected to the kob Argyrosomus hololepidotus (Sciaenidae), and two deeper water sparids, the silver Argyrozona argyrozona and the panga Pterogymnus laniarius (Hecht & Tilney 1989). While the contribution of barbel (G. feliceps & G. ater) to the catches prior to this study is unknown, it would appear that they have always formed a by-catch in the fishery (Port Alfred Commercial Fishermen's Association, pers. comm.), and their exploitation is likely to have increased steadily as a function of the continued expansion of the fishery.

During a preliminary assessment in 1984 it was found that although G. feliceps and G. ater occurred as a by-catch in the fishery, they collectively constituted approximately 10% of the total annual catch in terms of landed mass. This represented a harvest of between 35 and 40 tons per annum. The ratio of G. feliceps to G. ater in catches was approximately 3:1 (Hecht & Tilney op. cit.). While the fishery operated at various depths between 30 and 100 meters, the two ariids were generally not caught deeper than 60 meters. As a consequence of their familial life-history characteristics, particularly their low fecundity and extended parental care behaviour, it was anticipated that they would be vulnerable to over-exploitation in the short term if they were to become actively targeted for in the fishery. The objective of this stock assessment was to determine the impact of exploitation on the two K-selected barbel species in a fishery dominated by highly fecund r-selected sparids and sciaenids.

With the ever increasing demand for protein, it is probable that both G. feliceps and G. ater will become targeted for in the foreseeable future. They have high catchability in that they are voracious feeders, have a large gape and will take a baited hook under virtually any circumstances. They are commonly caught in conjunction with kob which forage over similar substrata and occur in the same depth-range. The weight of barbel in an average daily catch is far exceeded by that of kob, a larger species. The average kob:barbel weight ratio is 4.8:1. However, the catch in terms of numbers of fish landed is far more equable (1.3:1), and it is clear that on this basis the ariids, which have a fecundity several orders of magnitude lower than that of kob (pers. obs.), require special protection. It was anticipated that an investigation into their population dynamics at this relatively early stage in their commercial exploitation would enable the formulation of suitable management strategies before extreme, exploitation-related, population declines occurred. An understanding of the species' response to present levels of fishing effort will expedite future management policy decisions in which emphasis should be placed on acceptability to the fishery and ease of implementation.

An array of stock assessment models are available to the fisheries biologist and the type of model used depends on the nature of the information required (e.g. total biomass estimates or sustainable yield estimates). The models are particularly useful for predicting the responses of exploited populations to changes in fishing effort (Gulland 1977; Cushing 1981). Using the information from the models the fisheries biologist is able to propose, in terms of fishing effort, how the stocks should be managed. Subsequently, it is the task of fisheries administrators to weigh up the constraints of the resource against the socio-economic demands of the user community and to marry the two in the formulation of a management strategy for the fishery as a whole.

There are essentially two groups of models used in fish stock assessment. These are the surplus production, surplus yield or Schaefer type models (Schaefer 1954; Gulland 1977; Cushing 1981), and the dynamic pool, analytic or Beverton-Holt type models (Beverton & Holt 1957, Ricker 1975; Gulland op cit.; Cushing op cit.). The two categories of models differ considerably with respect to their basic data requirements. The surplus production models treat the population as a single entity, are based on a mathematical function describing total biomass regeneration (population growth), and require catch and effort data only. The dynamic pool models, on the other hand, treat the population as the sum of its individuals and deal explicitly with biological parameters affecting population abundance including growth, mortality and reproduction. The surplus production models are generally used when biological data are lacking, and when catch and effort data from several successive years are available. The dynamic pool models may be applied to data assimilated from one, or many years of fishing, and are considered to be more realistic due to their incorporation of detailed biological information (Ricker 1975, Gulland 1977, 1978, 1985, Cushing 1981, Everhart & Youngs 1981, Pitcher & Hart 1982).

A computer software programme using a Beverton & Holt-like dynamic pool model has been developed by the Department of Applied Mathematics at the University of Cape Town, specifically for use by the SANCOR[1] Marine Linefish community (Hughes 1986, Butterworth et al. 1989, Punt 1989, Punt & Hughes 1989). The assumptions of the model are as follows.

a) Recruitment is constant from one year to the next,
b) the stock is in an equilibrium state (biomass and age-structure are the same from one year to the next),
c) the population is closed (there is no immigration into or emigration from the stock), (Butterworth et al. 1989).

[1] South African Committee for Oceanographic Research.

The model utilises the total mortality rate of successive age classes in association with ages at sexual maturity and recruitment into the fishery to provide estimates of yield-per-recruit (Y/R), in terms of biomass. A sub-model of the yield-per-recruit model is the spawner biomass-per-recruit model (SB/R), which determines the proportion of spawners that remain in the fished population relative to the unexploited condition, as a function of age at first capture t_c, and fishing mortality F (Butterworth et al. 1989).

Independent estimates of total and natural mortality are required in order to determine the extent of fishing mortality. For the sake of convenience, instantaneous mortality rates (which apply over a short period of time during which the numbers in the population do not vary significantly), are used. This is done in order to avoid the algebraic complexity involved in the determination of mortality when the numbers of fish dying from one particular cause are affected by the numbers dying from any other cause (Gulland 1985). Another advantage of instantaneous rates of mortality is that they may be added to, or subtracted from, one another.

Since by tradition all barbel caught in the Port Alfred commercial fishery are the property of the crew members who caught them (Plate XIII), and since boat owners generally only weigh the proportion of the catch that is sold to whole-salers, only a very small percentage of the total annual barbel catch is ever recorded. The obligatory linefish catch return statistics furnished to the Sea Fisheries Research Institute in Cape Town could therefore not be used to determine annual landings in the Port Alfred area. Although sampling of total boat catches was undertaken in an attempt to estimate the percentage contribution by barbel, fishing regularly occurs at depths beyond that at which barbel occur, preventing accurate extrapolation of the total annual barbel catch on this basis. Estimates of abundance could therefore not be determined, nor

could virtual population analyses be utilised for estimation of trends in recruitment or mortality.

Plate XIII. Fisherman from the Port Alfred commercial fishery with the day's barbel catch. G. feliceps are held in his left hand and G. ater in his right hand.

A single estimate of total instantaneous mortality was determined for each population using combined length-frequency samples for the period 1985-1987. However, since fishing effort increased by approximately 17% during the study period from 2808 to 3375 boat-days per annum (Hecht & Tilney 1989), the estimates of instantaneous total mortality obtained for the fishery were probably slightly underestimated. Strictly

speaking, total mortality estimates should be determined using data from one year only. However, in the light of the slow growth exhibited by the two species, the assumptions of the model and the considerable variance attached to mortality estimation, the use of combined data from three successive years was considered acceptable.

Yield per recruit can, apart from several constant factors for example W_∞, t_0 and K, be mathematically described by three parameters, one of which describes the fish, and two which are characteristic of the fishery.

a) The parameter relating to the fish is the ratio of the growth coefficient (K), and natural mortality (M). The rate at which a fish approaches maximum size is dependent on both K and M, which therefore measure the rate at which the fish lives. In the calculation of yield curves, the M/K ratio tends to operate as a single parameter. A small M/K ratio indicates that the fish has a good chance of completing much of its potential growth before dying of natural causes, and the stock will contain many relatively large fish. A large M/K ratio suggests that fish are dying before much of their growth is completed and the stock should be fished at a relatively higher fishing effort and small recruitment size in order to gain the best yield from a given level of recruitment (Gulland 1985).

b) The parameters relating to the fishery are the amount of fishing, expressed as the ratio of fishing to natural mortality F/M, which is also the exploitation ratio E, where

$$E = F/(F+M)$$

c) The relative size at first capture c, where

$$c = l_c/l_\infty$$
$$= 1-\exp\{-K(t_c-t_0)\}$$

The Beverton-Holt equation for yield-per-recruit is therefore essentially a function of fishing mortality and age at first capture.

Materials & Methods

Since the growth curves for the sexes were found to be significantly different for both G. feliceps and G. ater the yield-per-recruit analyses were determined separately for the sexes (Beverton et al. 1984). This was considered particularly important for G. ater in which the size distribution of males in the fishery was noticeably smaller than that of females. In addition, the male mouth-brooding habit of the barbel species is likely to cause differences in catchability, and hence mortality, between the sexes at certain times of the year. As males do not feed whilst mouth-brooding they will theoretically not be subject to fishing mortality during this period, which lasts between four and five months. This provided additional motivation for modeling the sexes separately (A. Punt, Department of Applied Mathematics, University of Cape Town, pers. comm.).

In the previous chapter it was shown that the Schnute growth model provided the curves of best fit for observed G. ater growth. However, since the von Bertalanffy growth parameters, K and L_∞, are extensively used in dynamic pool-type modeling, growth of G. ater was recalculated using the von Bertalanffy growth model.

Mortality determination

Total mortality (Z): Several techniques are available for the determination of total mortality. Three were used in this study.

a) Catch-curves: Age-length keys were constructed using two different methods. In the first, a sub-sample of fish were

aged, and the age-length key normalised with respect to the length frequency distribution of the total sample using matrix multiplication (Hughes 1986, Butterworth et al. 1989). The normalised age-length key was then used in the construction of a catch-curve, in which the natural log of fish number was plotted against age as follows:

$$\log_e N = a + bt$$

where the value of 'b', with the sign changed is representative of total mortality, Z (Ricker 1975). An example of the method used in the normalisation of the age-length keys is provided in Appendix IIIa.

In the second instance the von Bertalanffy growth equation was used to determine the mean relative ages of fish in successive size classes (Pauly 1983). These were then plotted against the adjusted number of fish in each size class as follows:

$$\log_e(N/dt) = a + bt$$

where dt = the time taken to grow from the lower (t_1) to the upper limit (t_2) of a given size class,
t = the relative age corresponding to the mid-range of the length class in question.

An example of the above methodology is provided for G. feliceps males in Appendix IIIb.

b) The Robson & Chapman (1961) method which computes survival S, in which the number of animals alive at successive ages are determined using the formula:

$$S = T/n+T-1$$

where T = a statistic,
n = sample size.

Mortality is determined from survival as follows:

$$Z = -\text{Log}_e\ S.$$

c) A method proposed by Beverton & Holt (1956, in Butterworth et al. 1989) which determines total mortality from the relationship between the age at recruitment to the fishery and the mean age of fish in the catch as follows:

$$Z = [1 + 1/a - a_f)]$$

where a = mean age of all fully recruited fish sampled,

a_f = age at full recruitment into the fishery.

Natural mortality (M): Natural mortality incorporates death through predation, disease and other natural causes, and is readily determined using several different equations, four of which are used here.

a) Pauly (1980). Pauly found that natural mortality was correlated with longevity, and hence K, and also with size and water temperature. He expressed these interrelationships in the form of a multiple regression as follows:

$$\text{Log}_{10}\ M = -0.0066 - (0.279\ \text{Log}_{10}\ L_\infty) + (0.6543\ \text{Log}_{10}\ K) + (0.4634\ \text{Log}_{10}\ T)$$

where L_∞ = theoretical maximum length,

K = Brody growth coefficient,

T = mean annual bottom temperature.

b) Gunderson & Dygert (1988). This is an empirical formula derived from regression of gonad index against values of M obtained from the literature to give the relationship:

$$M = (1.68 \times WGSI) + 0.03$$

where WGSI = a wet gonadosomatic index (gonad wt./body wt.)

c) Rikhter & Efanov (1977). This is also an empirically derived formula based on the relationship between natural mortality and age at sexual maturity as follows:

$$M = 1.521/(0.7t_m) - 0.155$$

where t_m = age at 50% maturity.

d) Roff (1984). An empirical formula relating natural mortality to growth rate and age at sexual maturity as follows:

$$M = 3 \times K[\exp(-KT)]/1 - \exp(-KT)$$

where K = Brody growth coefficient,
T = age at sexual maturity.

Fishing mortality (F): Instantaneous rates of fishing mortality were derived by subtracting natural mortality estimates from the total mortality estimates, i.e. from the equation:

$$F = Z - M.$$

Selectivity

Although the selectivity curves for barbel were logistic, knife-edge selectivity was assumed for the fishery to enable the use of the computer software programme PC-VONBERT (Punt

1989) for the calculation of percentage survival, yield-per-recruit and spawning biomass-per-recruit. The implications of the above are discussed later.

Yield-Per-Recruit Analysis

The Beverton-Holt (1957), like yield-per-recruit models used by the PC-VONBERT programme, analyse the trade-off between the increase in mass of individual fish and the decrease in the size of a cohort with time. The following assumptions apply:

a) Recruitment is constant from one year to the next,

b) the stock biomass and age structure is in equilibrium,

c) there is no immigration of individuals into or emigration out of the stock (Hughes & Punt 1988).

The following sub-models were used:

a) Yield-per-recruit.

$$Y/R = Fw_{\infty}e^{-Mt_c}\left[\frac{1}{(M+F)} - \frac{3e^{-k(t_c - t_0)}}{(M+F+k)} + \frac{3e^{-2k(t_c - t_0)}}{(M+F+2k)} - \frac{e^{-3k(t_c - t_0)}}{(M+F+3k)}\right]$$

where Y/R = yield-per-recruit (in terms of mass),

W_{∞} = theoretical maximum weight,

t_c = age at first capture (50% recruitment),

t_0 = theoretical age at which length = 0,

K = Brody growth coefficient,

F = instantaneous rate of fishing mortality,

M = instantaneous rate of natural mortality.

b) The rate of change of numbers in a cohort with time (survival),

$$dN(t)/dt = (-M - S(t)F) \times N(t)$$

where $N(t)$ = the number of t-year old fish in the population,

M = the instantaneous rate of natural mortality,

F = the instantaneous rate of fishing mortality,

$S(t)$ = the selectivity of the fishing gear on fish of age t.

c) Spawner biomass-per-recruit.

(i) for $t_m \geq t_c$ (*G. feliceps* males),

$$SB/R = w_\infty e^{-Mt_m - F(t_m - t_c)} \left[\frac{1}{(M+F)} - \frac{3e^{-k(t_m - t_0)}}{(M+F+k)} + \frac{3e^{-2k(t_m - t_0)}}{(M+F+2k)} - \frac{e^{-3k(t_m - t_0)}}{(M+F+3k)} \right]$$

(ii) for $t_m < t_c$ (*G. feliceps* females, *G. ater* males & females):

$$SB/R = w_\infty \left[\frac{(e^{-Mt_m} - e^{-Mt_c})}{M} - \frac{3e^{kt_0} \cdot \left[e^{-(M+k)t_m} - e^{-(M+k)t_c}\right]}{(M+k)} + \frac{3e^{-2kt_0} \cdot \left[e^{-(M+2k)t_m} - e^{-(M+2k)t_c}\right]}{(M+2k)} - \frac{e^{-3kt_0} \cdot \left[e^{-(M+3k)t_m} - e^{-(M+3k)t_c}\right]}{(M+3k)} \right] + \frac{Y_m}{FR}.$$

where SB/R = spawning biomass-per-recruit,

t_m = age at 50% sexual maturity,

y_m = yield in terms of mass,

R = recruitment

The programme also calculates the following management variables:

a) F_{MSY}, the level of fishing effort at which maximum sustainable yield is attained.

b) $F_{0.1}$, the level of fishing effort at which the marginal yield-per-recruit drops to 10% of its value for the unexploited stock. Increasing F beyond $F_{0.1}$ provides a very small return in terms of yield-per-recruit in relation to the increased costs associated with a higher F.

c) $F_{50\%SB}$, the level of fishing mortality at which 50% of the population spawner biomass remains.

Results

Mortality estimation

The percentage length-frequency distributions and catch-curves for G. feliceps and G. ater males and females are presented in Figures 58, 59, 60 & 61. The regression lines used to determine total mortality are plotted on the catch-curves. The length-frequency curves for G. feliceps indicated that males and females were equally represented in all of the size classes. In contrast, the G. ater length-frequency distribution was bi-modal and indicated that females survived to a much larger mean size than males. This bi-modal size distribution was probably a function of the slower growth rate exhibited by males. Males reached sexual maturity at approximately the same size, although a year later in life than females. The disparity in growth rate might have been a response to the high energetic requirements associated with mouth-brooding in males.

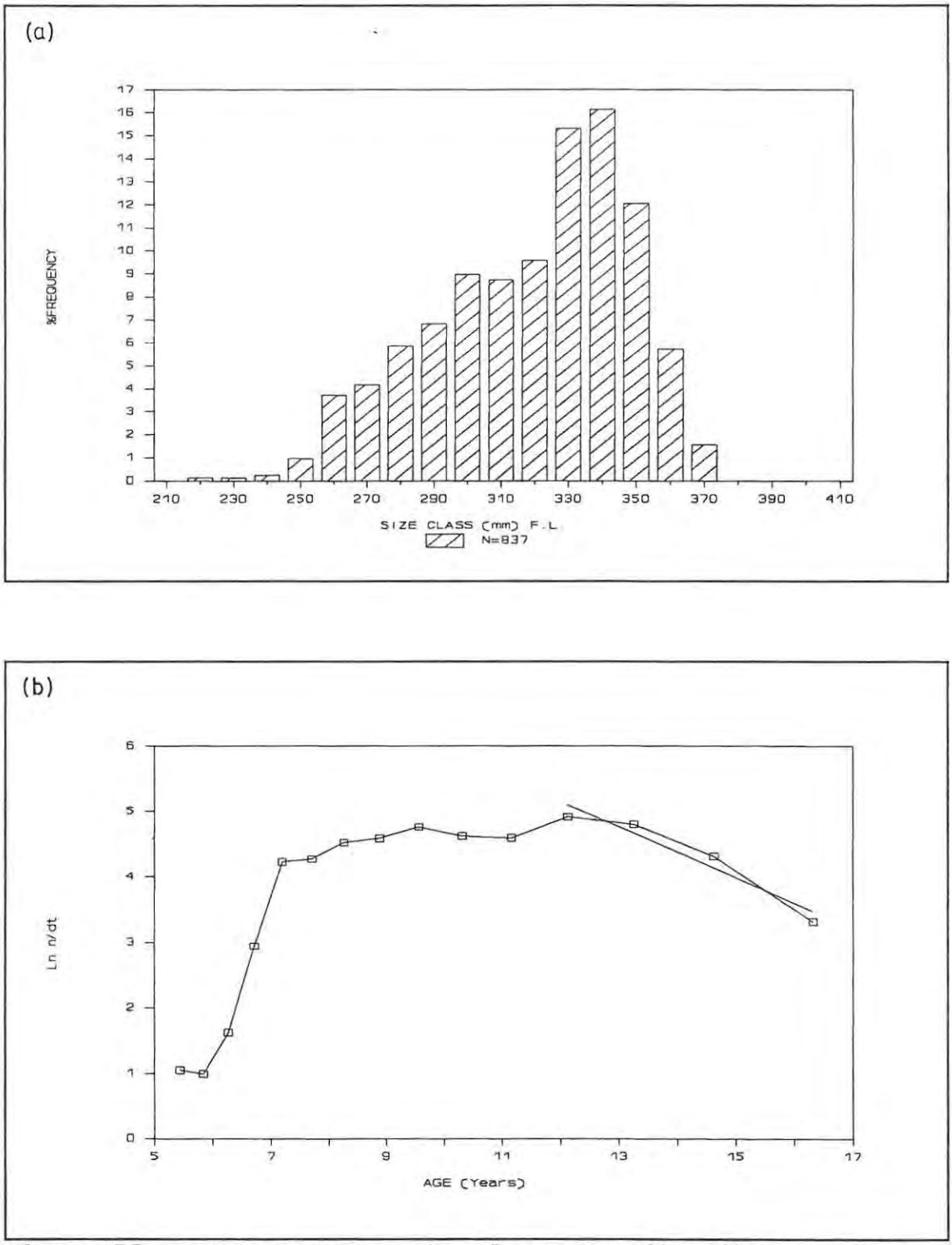
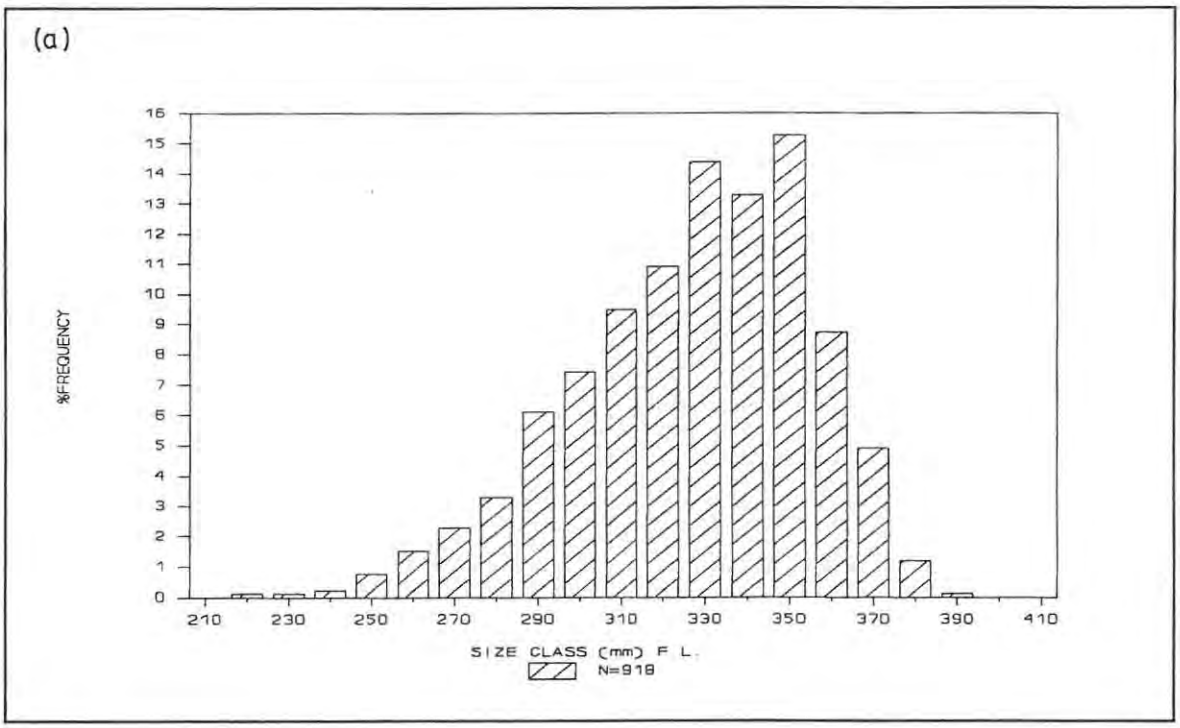


Figure 58. (a) Percentage size frequency distribution and (b) catch-curve and regression line for G. feliceps males.



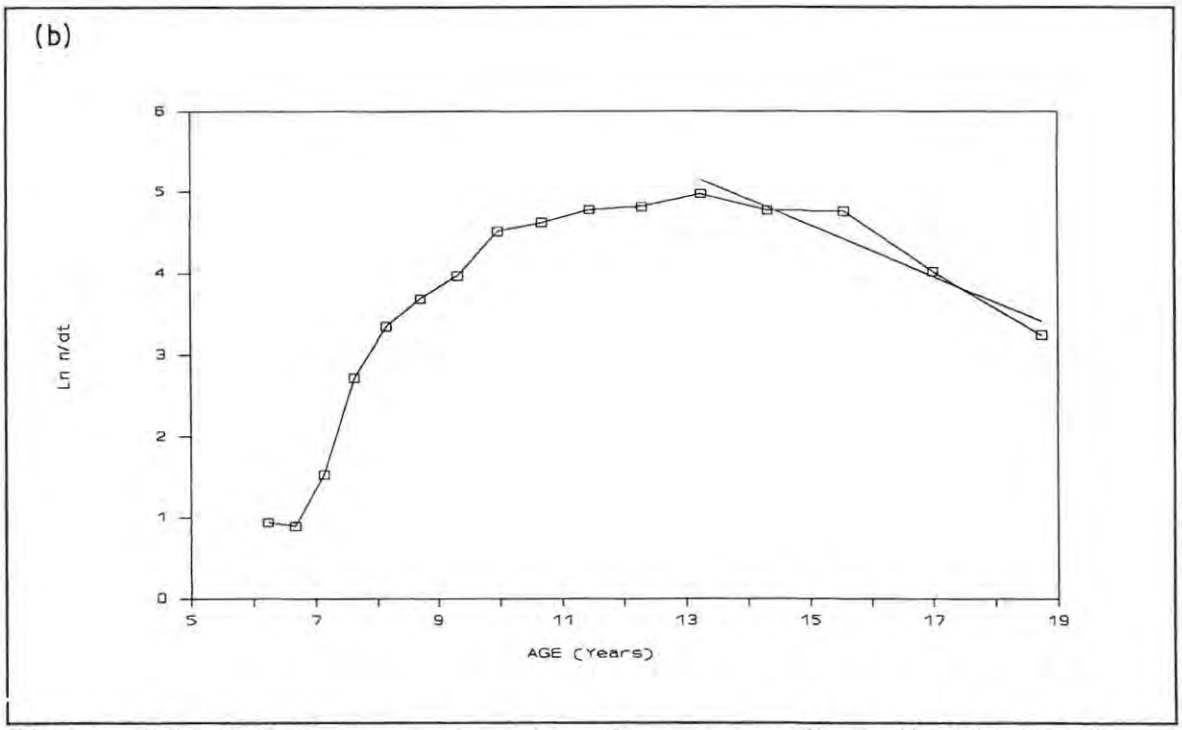


Figure 59. (a) Percentage size frequency distribution and (b) catch-curve and regression line for G. feliceps females.

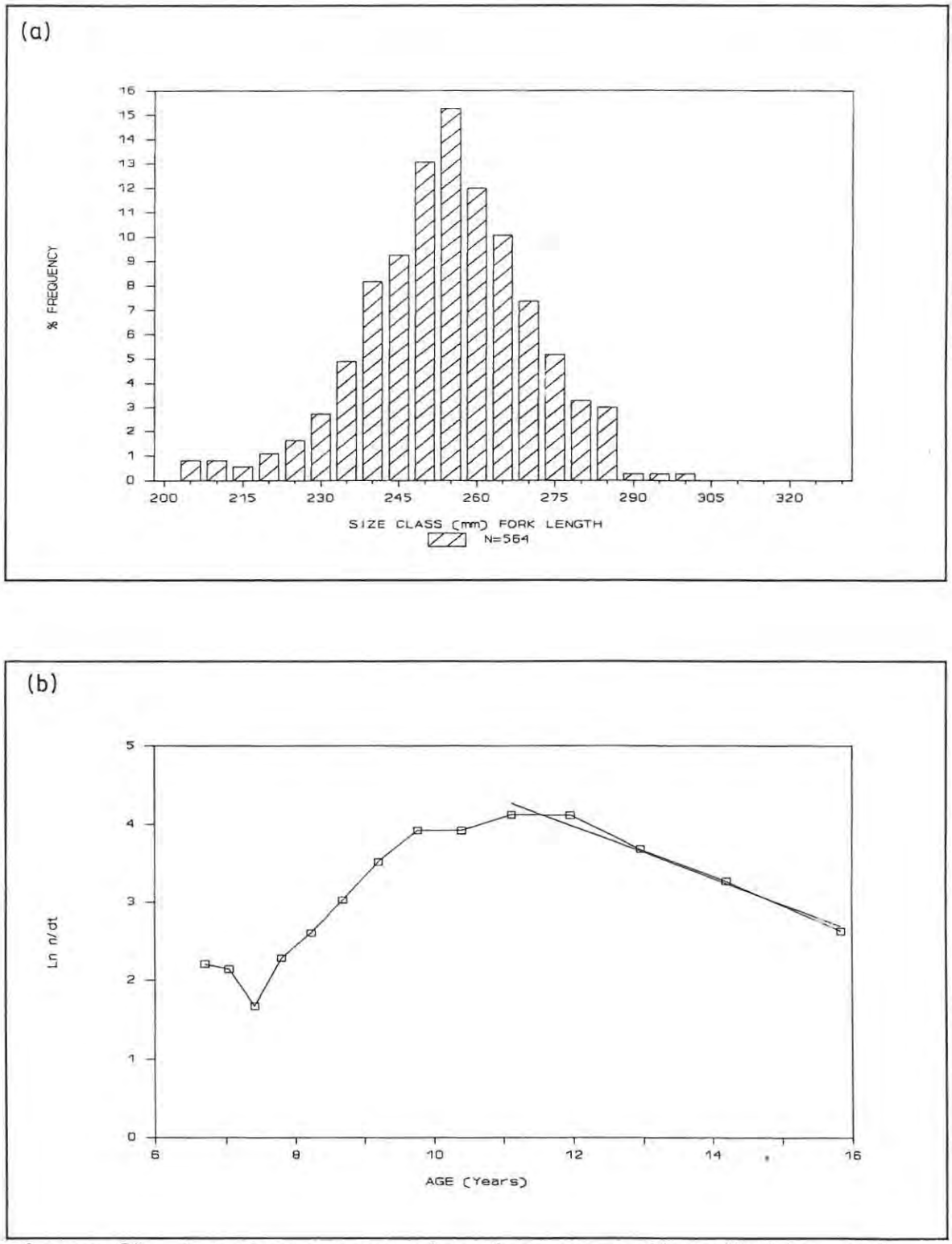
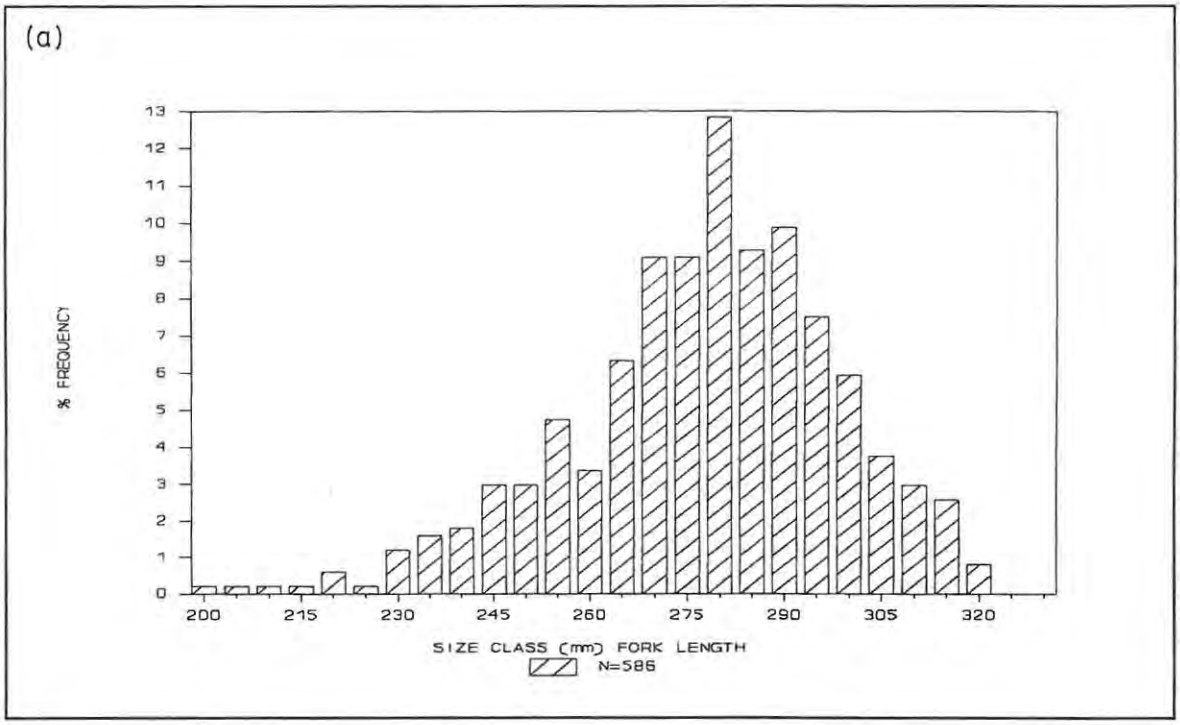


Figure 60. (a) Percentage size frequency distribution and (b) catch-curve and regression line for G. ater males.



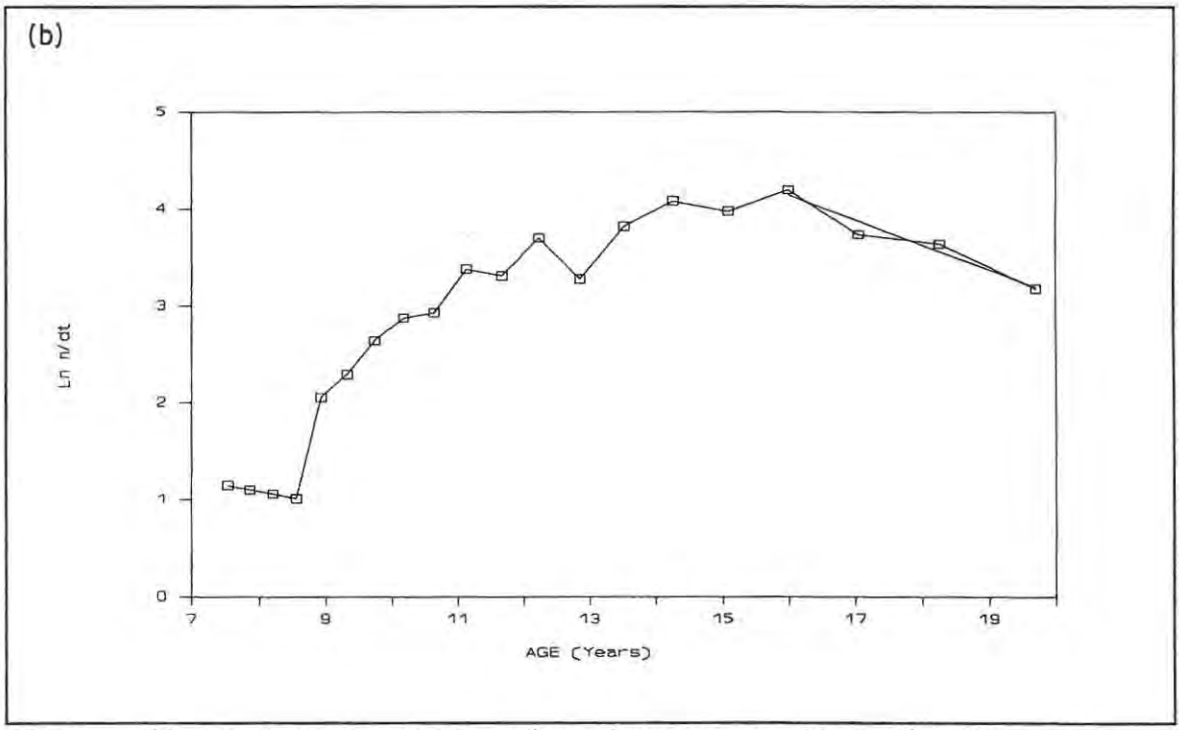


Figure 61. (a) Percentage size frequency distribution and (b) catch-curve and regression line for G. ater females.

The instantaneous total and natural mortality rates are presented in Tables XXIV & XXV, and demonstrate the considerable variation in the estimates obtained. In Table XXIV, the Ricker[1] and Ricker[2] methods of total mortality estimation are those using normalised age-length keys and total length-frequency distributions respectively.

Table XXIV: Instantaneous total mortality rates (Z), using four different methods. Variance estimates appear in parentheses.

	CHAPMAN-ROBSON (1961)	RICKER[1] (1975)	BEVERTON & HOLT (1956)	RICKER[2] (1975)
G. FELICEPS MALES	0.369 (0.024)	0.183 (0.106)	0.249 (0.042)	0.390 (0.075)
G. FELICEPS FEMALES	0.268 (0.015)	0.229 (0.067)	0.223(0.039)	0.318 (0.056)
G. ATER MALES	0.445 (0.041)	0.234 (0.086)	0.284 (0.070)	0.334 (0.032)
G. ATER FEMALES	0.613 (0.047)	0.360 (0.174)	0.285 (0.064)	0.257 (0.043)

Table XXV: Estimates of instantaneous natural mortality rates (M), using four different methods.

	GUNDERSON & DYGERT (1988)	PAULY (1980)	RIKHTER & EFANOV (1977)	ROFF (1984)
G. FELICEPS MALES	0.200	0.137	0.248	0.136
G. FELICEPS FEMALES	0.200	0.101	0.279	0.188
G. ATER MALES	0.170	0.211	0.279	0.130
G. ATER FEMALES	0.170	0.133	0.321	0.239

There were no noticeable trends in total or natural mortality estimation using the different methods, i.e. one method did not result in consistently lower or higher estimates than any other. It was decided that the use of mean values representative of all the methods used in mortality estimation should be avoided, as these would simply have compounded the variances of the individual methods without increasing

precision. Instead, a result given by one method, for Z and M respectively, was chosen for use in the yield-per-recruit models. The models were therefore interpreted with due cognisance of the high degree of variance associated with the mortality estimation.

For Z, the method of Ricker[2] (Table XXIV) was chosen for the following reasons:

a) The Ricker[1] method, which is based on normalised age-length keys, produced catch-curves in which the oldest age classes were inaccurately represented. This was a result of poor sampling procedure in which differences between the size-frequency of the sub-sample of aged fish and the total size-frequency sample from the fishery, gave rise to considerable bias in the older age classes during the normalisation procedure (Appendix IIIa).

b) The Robson-Chapman method was based on the same data set as (a) above, and was therefore rejected.

c) The Beverton-Holt method did not consider either the age-frequency or length-frequency distributions and was therefore considered to be inferior to the Ricker[2] method.

d) The Ricker[2] method utilised the descending limb of the length-frequency distribution curve of the total sample, and was therefore the most representative method for the determination of Z.

For natural mortality, the estimates derived using the Pauly (1980) method were used. Although the variance in the value of M obtained using this method ranges between 0.3 and 3 times the estimate (Butterworth et al. 1989), it was chosen because of its general use in the literature. In order to compensate for the variance associated with M, stock simulation was performed

for natural mortality values 25% above and below the formula estimate.

The chosen values of Z, M and F, together with the age and growth parameters used in the yield-per-recruit analyses, are presented in Table XXVI.

Table XXVI: Parameters used in the yield-per-recruit analyses (t_c = age at 50% recruitment, t_m = age at 50% sexual maturity).

	L_∞	K	t_0	t_c	t_{sm}	Z	M	F
G. FELICEPS MALES	389.9	0.147	-1.406	9.46	9.82	0.390	0.137	0.253
G. FELICEPS FEMALES	407.5	0.120	-1.813	11.01	8.91	0.318	0.101	0.217
G. ATER MALES	285.9	0.193	-1.289	9.46	8.78	0.334	0.211	0.123
G. ATER FEMALES	321.3	0.132	-2.554	11.97	7.41	0.257	0.133	0.124

Sex ratios

Because males were effectively excluded from the fishery during the mouth-brooding period, sex ratios were determined independently for the period encompassing spawning and mouth-brooding. They were also determined separately for the sexually mature sector of the populations (Table XXVII).

The sex ratios for sexually mature animals revealed that there were significant differences throughout the year for G. feliceps, but only during the spawning season for G. ater. This indicated that the mature G. feliceps male population might be considerably smaller than that of the mature female population, or that a proportion of the mature male population occupy a habitat in which they are not exploited by the fishery.

Sex ratios for entire populations revealed that while there was, as expected, a significant difference between the numbers of male and female G. ater caught during the spawning and

mouth-brooding period, this was not the case for G. feliceps. A high juvenile component in the catches masked the absence of mouth-brooding males during this time. The percentage representation of mature animals in the catches is presented in Table XXVIII for the two species.

Table XXVII: Sex ratios for G. feliceps and G. ater. Adjusted Chi-square tests were used to determine significant differences between the sexes at the 95% level.

	Mature pop. (Male:Female)	Chi-sq. (df = 1)	Sig. dif. (Yes/No)	Whole pop. (Male:Female)	Chi-sq. (df = 1)	Sig. dif. (Yes/No)
			G. FELICEPS			
Spawning season	1:1.65	18.888	Yes	1:1.11	1.262	No
Off season	1:1.51	12.360	Yes	1:1.03	0.074	No
			G. ATER			
Spawning season	1:2.23	62.77	Yes	1:2.10	28.09	Yes
Off season	1.09:1	0.705	No	1.11:1	1.035	No

Table XXVIII: The percentage representation of mature G. feliceps and G. ater males and females in catches.

	Males	Females
	G. FELICEPS	
Spawning season	56%	82%
Off season	60%	88%
	G. ATER	
Spawning season	94%	99%
Off season	96%	97%

Yield-per-recruit analyses

The percentage recruit survival curves indicate that for G. feliceps, between 68% and 71% of the recruits from any

particular year-class will have succumbed through natural causes before they are recruited into the fishery (Fig. 62). Similarly for G. ater, between 79% and 85% of the fish die before they are exposed to exploitation (Fig. 63). The curves indicate that both species might be fished more efficiently if they were recruited into the fishery at an earlier age. It should be noted, however, that in the extrapolation of survival curves back to age zero, the model uses total mortality values which were determined using only the larger size classes. Mortality amongst the smallest size classes is in reality far higher, and the percentage survival values determined by the model are probably over-estimates.

The plots of yield-per-recruit (Y/R) vs. age at first capture (t_c) also indicated that t_c should be reduced. They demonstrated that maximum yields for G. feliceps would be attained at ages between 5 and 7 years for males, and 6 and 9 years for females (Fig. 64). G. ater males and females should be recruited at ages between 2 and 4 years, and 3 and 5 years respectively for maximum sustainable yields to be realised (Fig. 65).

The spawner biomass-per-recruit (SB/R) vs. fishing mortality (F) curves indicate that G. feliceps are being fished beyond 0.5K, the optimum level (Schaefer 1954; Butterworth et al. 1989) at which 50% of the initial spawner biomass remain (Fig. 66). Males are fished at between 0.25K and 0.33K, and females between 0.22K and 0.24K. Galeichthys ater males are fished between 0.43K and 0.67K, and females between 0.5K and 0.56K, indicative of a more healthy spawner biomass (Fig. 67).

The yield-per-recruit vs. fishing effort curves reflect the results of the spawner biomass-per-recruit curves, in that present levels of fishing effort for G. feliceps are higher than the recommended $F_{0.1}$ value in both the male and female populations (Fig. 68). Females are exploited more heavily than males. In G. ater, however, present fishing effort occurs below the $F_{0.1}$ value for both sexes (Fig. 69).

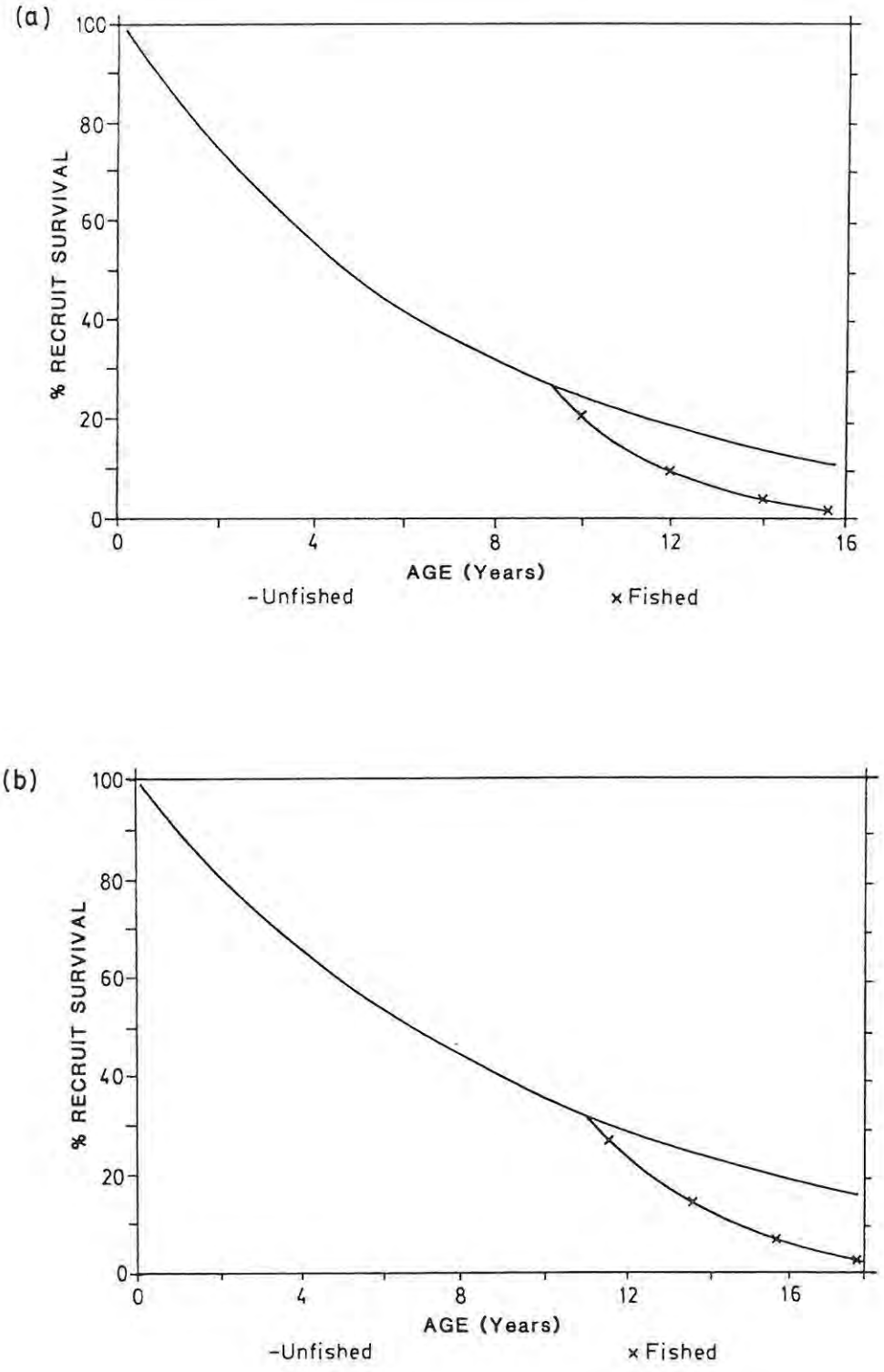


Figure 62. Percentage recruit survival vs. age curves for fished and unfished (a) G. feliceps male and (b) female populations.

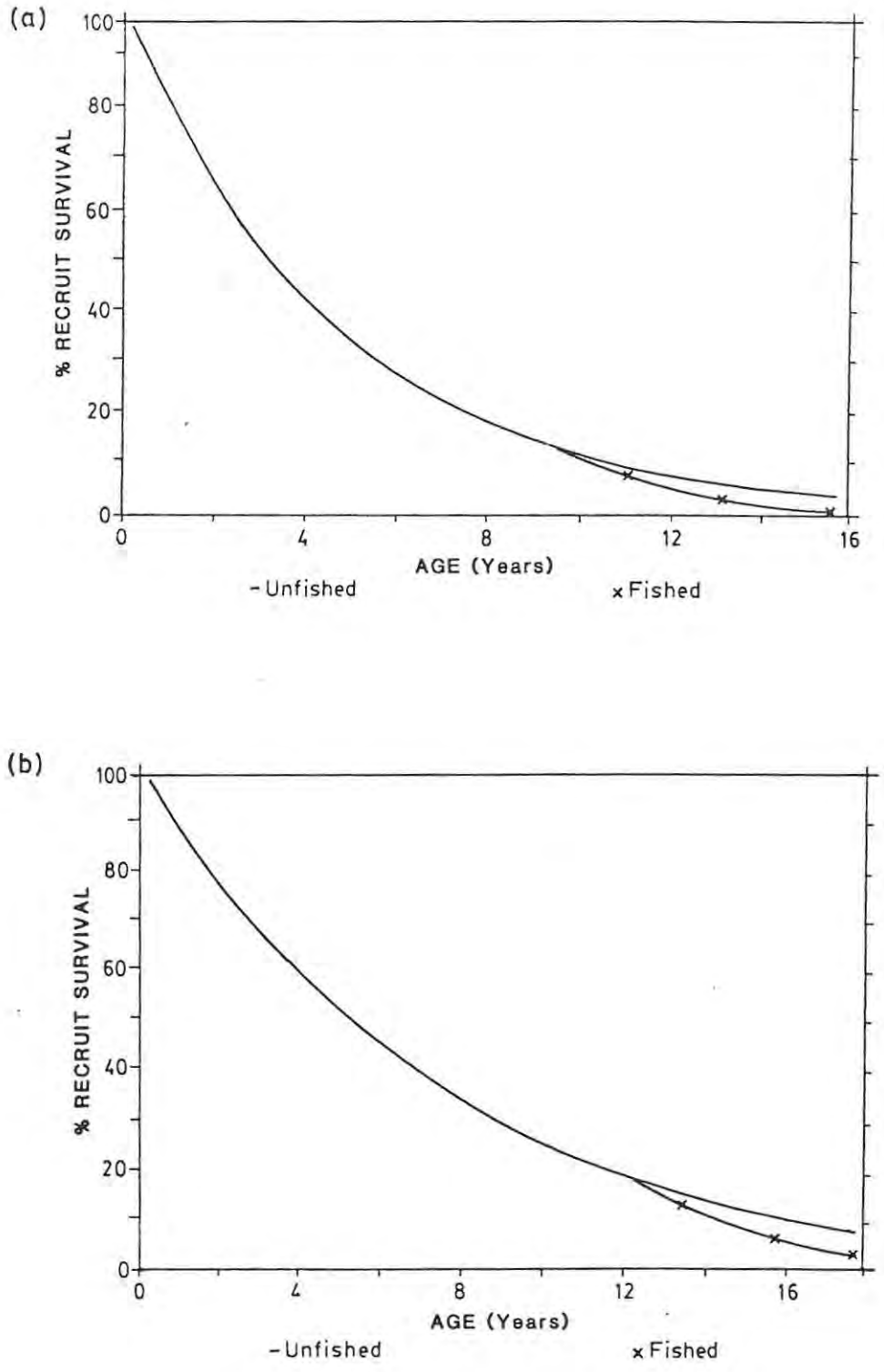
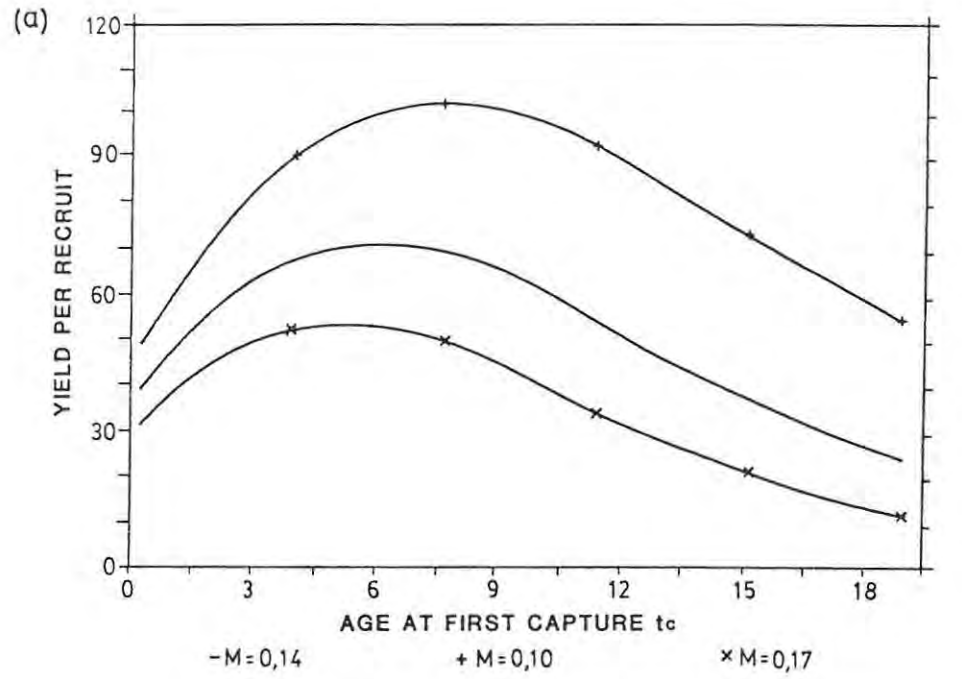


Figure 63. Percentage recruit survival curves vs. age for the fished and unfished (a) G. ater male and (b) female populations.



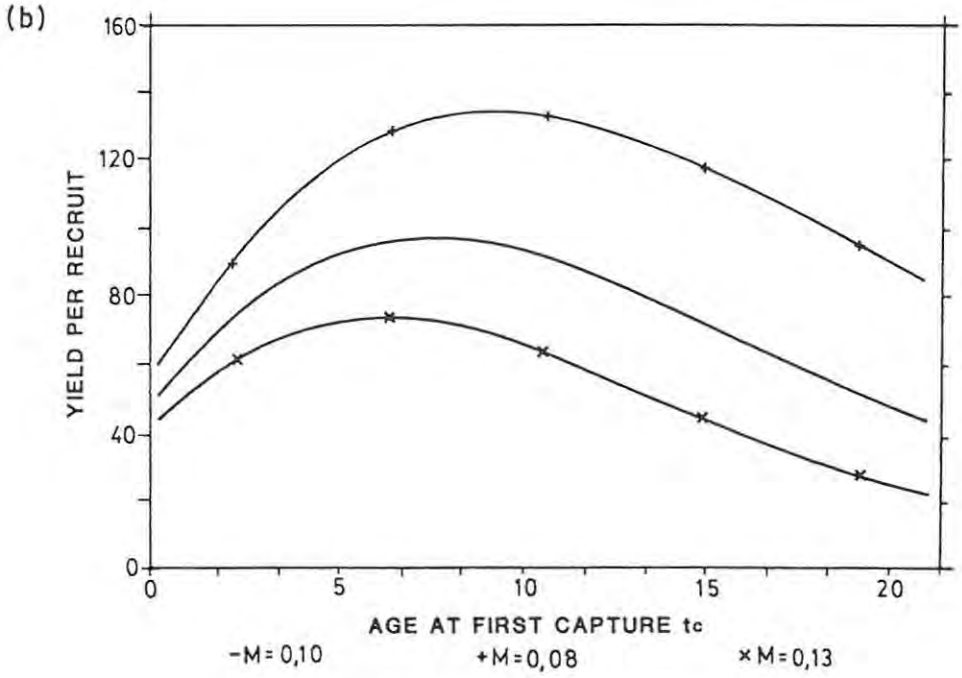


Figure 64. Yield per recruit vs. age at first capture (t_c) curves for the (a) G. feliceps male and (b) female populations, plotted using three different values for natural mortality (M).

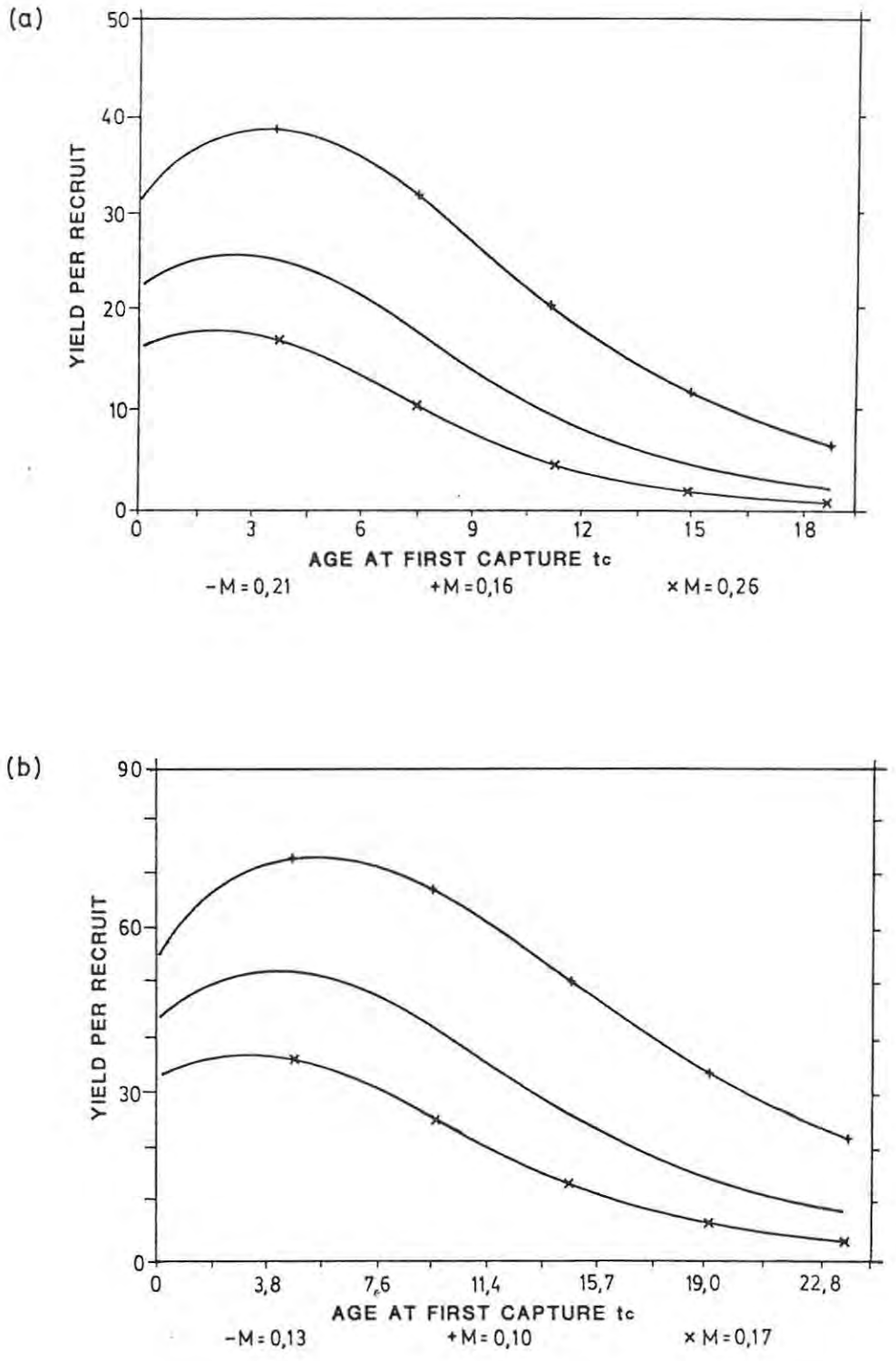


Figure 65. Yield per recruit vs. age at first capture (t_c) curves for (a) G. ater males and (b) females, plotted using three different values for natural mortality (M).

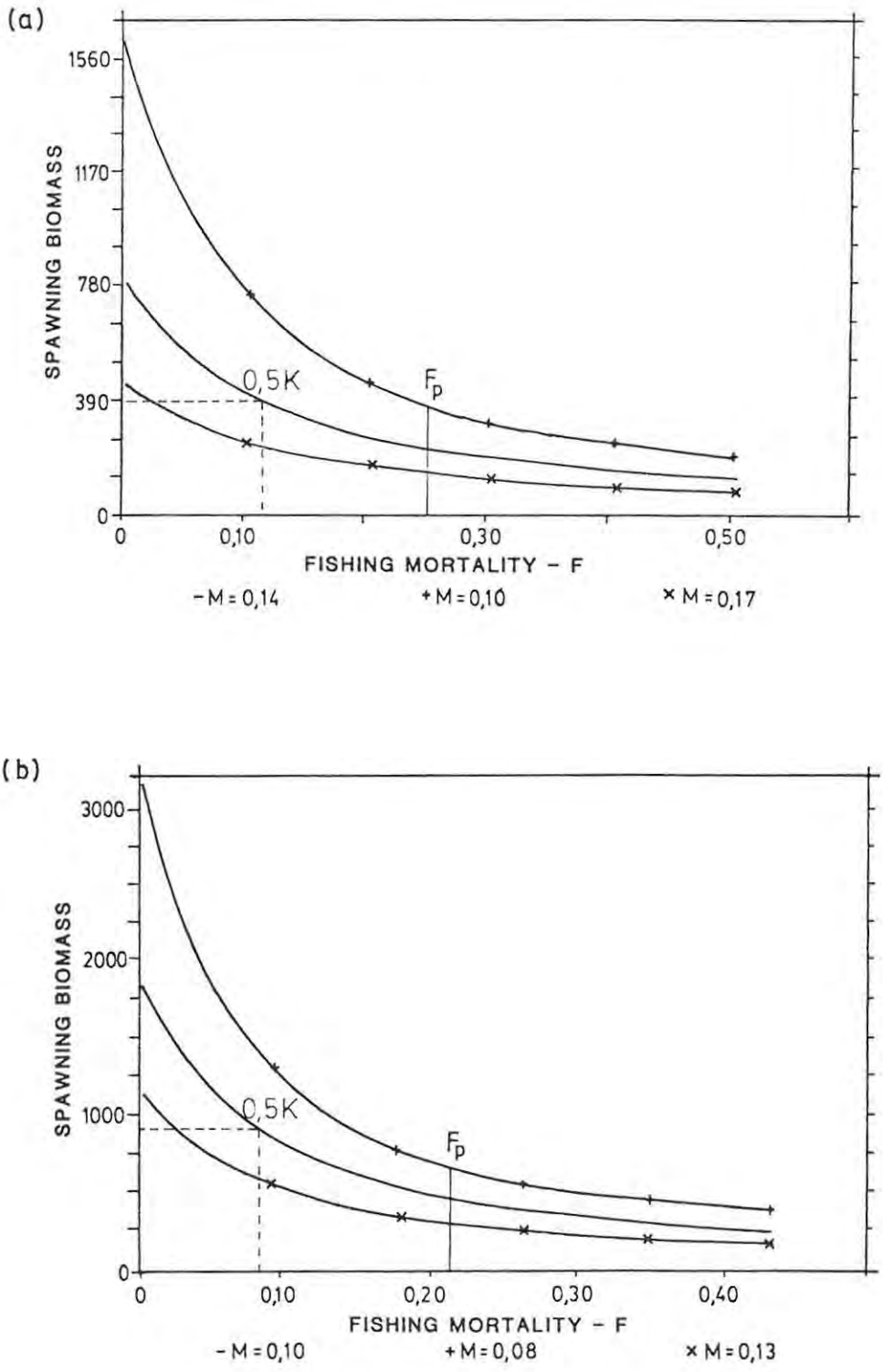


Figure 66. Spawner biomass per recruit vs. fishing mortality (F) curves for (a) G. feliceps males and (b) females, plotted for three values of natural mortality (M). F_p = present fishing effort.

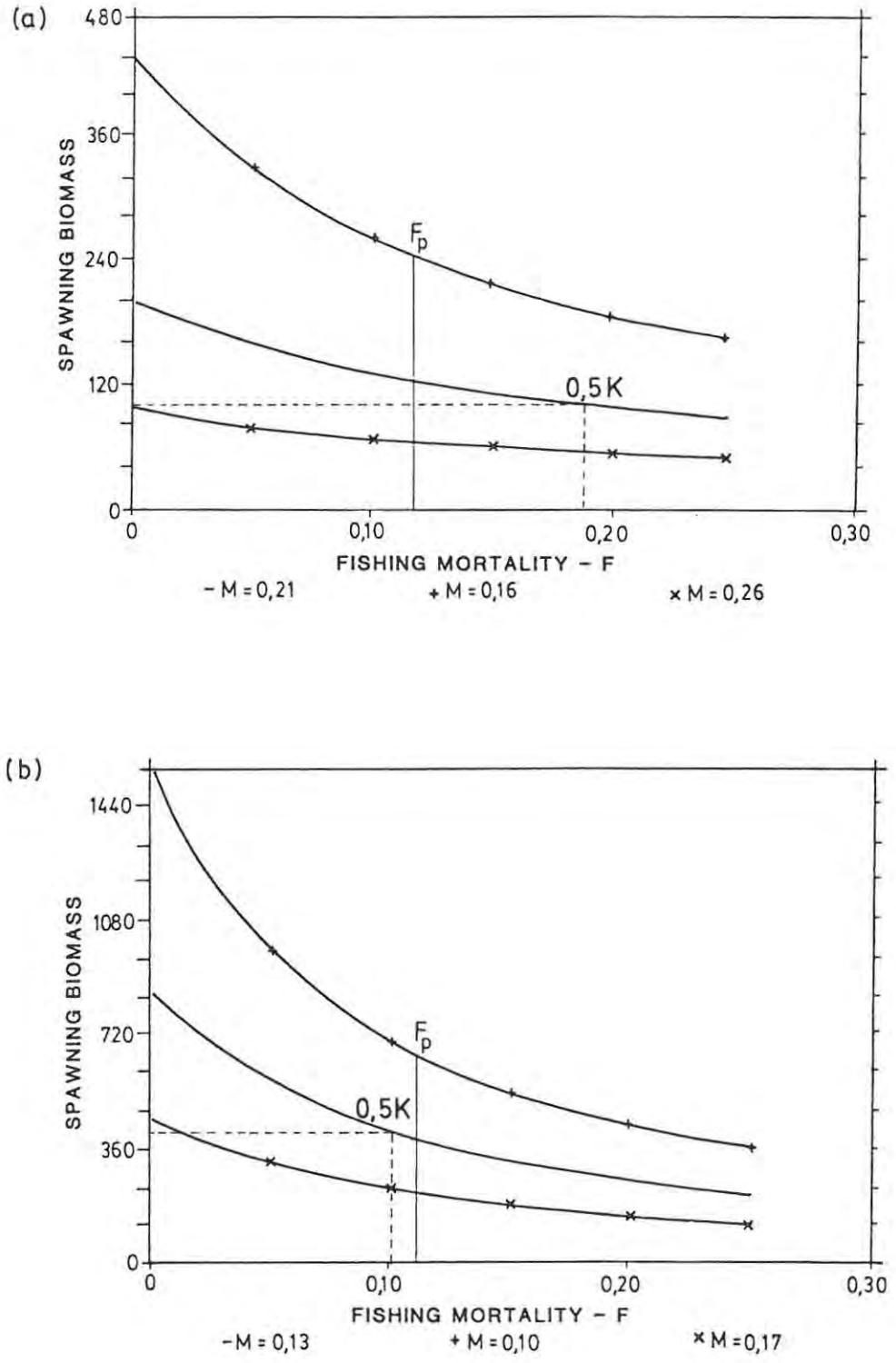


Figure 67. Spawner biomass per recruit vs. fishing mortality (F) curves for (a) G. ater males and (b) females, plotted for three values of natural mortality (M). F_p = present fishing effort.

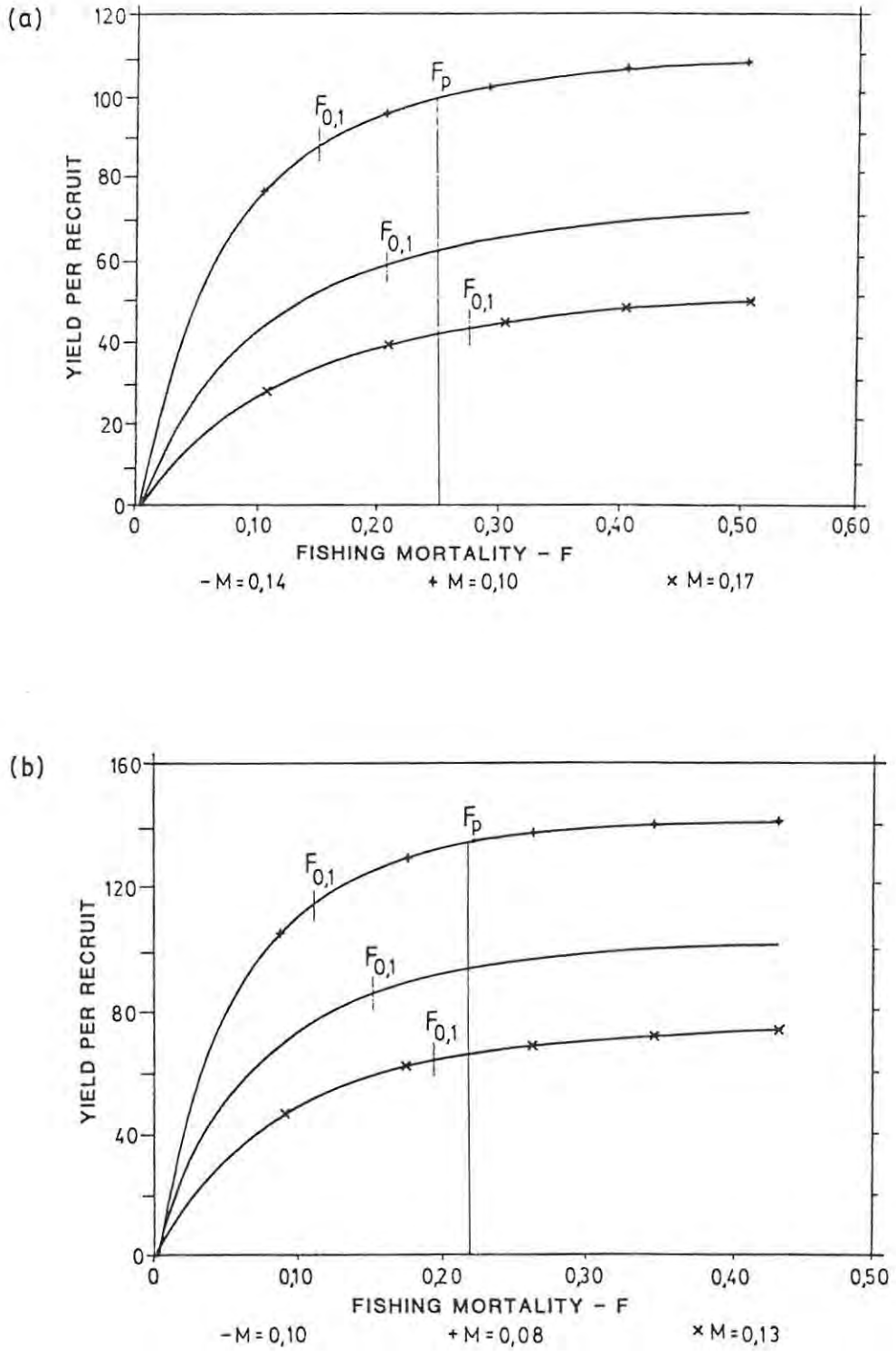


Figure 68. Yield per recruit vs. fishing mortality (F) curves for (a) G. feliceps males and (b) females, plotted for three different values of natural mortality (M). F_p = present fishing effort.

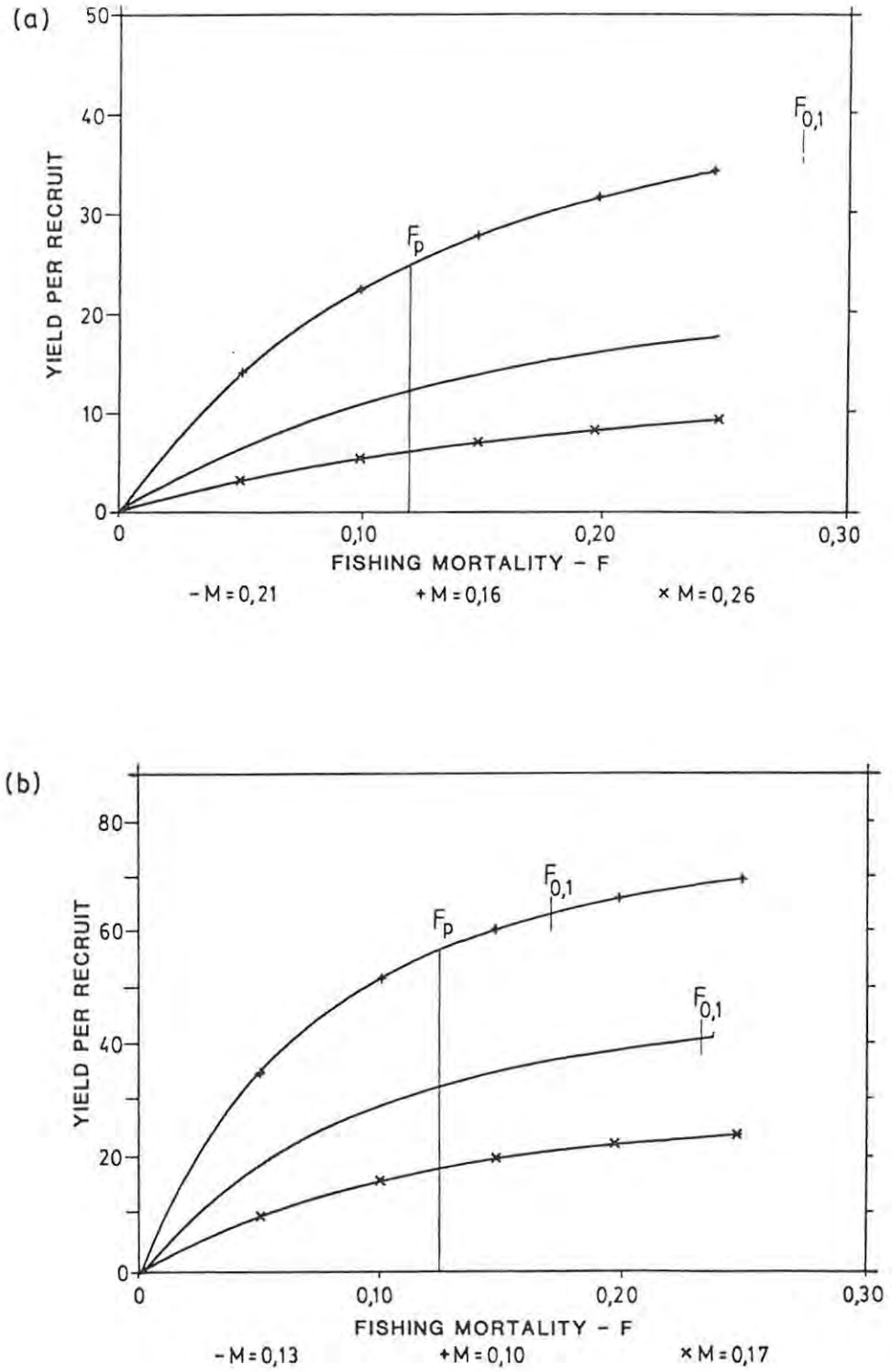


Figure 69. Yield per recruit vs. fishing mortality (F) curves for (a) G. ater males and (b) females. F_p = present fishing effort.

Discussion

The effect of gear on a fished population, i.e. the pattern of fishing mortality, is termed selectivity. Three types of selectivity are recognised, namely knife-edge, logistic and normal (Punt & Hughes 1989). The simplest method, and the one used in the available computer software programmes, is knife-edge selectivity which assumes that fish become available to the fishery at a particular age and that no fish younger than this age are caught. Assuming knife-edge selectivity and constant recruitment from one year to the next the catch-curve will show an exponential decline, the slope of which is determined by the total mortality rate (Butterworth et al. 1989, Punt & Hughes 1989). The recruitment, or selectivity curves, for the two barbel species in the linefishery were logistic. Starting with fish approximately 200mm in length, catches increased smoothly with increasing fish size and reached a maximum in the larger sizes classes. However, the calculation of total mortality using catch-curves was undertaken using only the size classes larger than that at which peak recruitment occurred. Several age classes were thus eliminated from the mortality estimation and in so doing, knife-edge selectivity was artificially imposed on the data. In order to improve precision by taking the full range of age data into account using a more realistic model, additional parameters need to be estimated. Butterworth et al. (op. cit.), however, state that the use of such models, in which increased numbers of parameters require simultaneous estimation from the same data set, may not necessarily lead to increased precision. Punt (Dept. Applied Mathematics, University of Cape Town, pers. comm.) emphasised the importance of determining whether there is a substantial difference between assuming knife-edge or logistic selectivity. For the purposes of this preliminary stock assessment, knife-edge selectivity was accepted in the light of its simplicity and ease of application to the available yield-per-recruit models. However, the final estimates of Z, and hence F, are likely to have poor precision.

Catch-curves may be considerably biased if incorrectly constructed (Pauly 1983), or if the numbers of fish caught at any age included in the subsequent regression are low (Butterworth et al. 1989), and they should be used with caution. Skewed catch curves lead to poor estimates of total and, hence, fishing mortality. Ricker (1975) cautions against the use of age-length keys unless the fish used for the age determination come from the same stock, during the same season and using the same fishing gear as those used to take the length-frequency samples. In short, he recommends that more effort be invested in ageing large samples of fish rather than in generating massive length-frequency data-banks, unless the latter are to be put to some other additional purpose. In this study catch-curves derived from the normalisation of age-length keys using length-frequency samples did result in biases in numbers at age for the oldest age-classes, and had to be rejected. The frequency of aged fish in the age-length key should exactly reflect the total size-frequency distribution of the sampled population if accurate catch-curves are to be constructed. Pauly (1983) warned that when utilising length-frequencies to construct catch-curves (Ricker[2] method in Table I), the incorporation of fish sizes close to that of the population asymptotic size should be avoided since the ages obtained for these fish may be grossly over-estimated. He emphasised the importance of visual examination of the plotted catch curve in order to identify the portion of the descending limb that may be used to calculate Z effectively.

Several workers have developed models which correlate natural mortality to life history parameters such as age at sexual maturity, costs of reproduction, growth rate and maximum age (see Vetter 1988 for review). Since these models all produce a single estimate of M for the stock, they are essentially no more than broad estimates (Vetter op. cit.), and should be used with caution when applied to fishery models. In general, the results of this study have shown that the higher the estimates of M, the lower the estimates of Y/R_{max} and the age at first

capture. More accurate methods for determining M utilise catch analyses and predation methods (Vetter op. cit.), both of which are based on cohort analysis and which require accurate catch data from several successive years. The duration of the present study precluded the use of cohort analysis.

The accuracy of the yield-per-recruit curves will vary according to the degree of confidence with which the component parameters were established. The evaluation of stock condition is therefore largely reliant on representative estimates of growth rate and mortality. While the growth model parameters are fairly accurate in that they are able to realistically describe observed growth patterns, the widely ranging mortality estimates generated by the methods used in this study clearly are not. Two obvious deductions can be drawn from the above. Either the methods are poor and fail to adequately reflect real mortality, or the input data were inadequate. In all probability, both deductions apply. The results of the yield-per-recruit analyses should therefore be considered with the limitations of the mortality estimates in mind and be used with caution. Nevertheless, they are acceptable for use in preliminary stock assessments which seek to detect trends in population structure and to provide guide-lines for management alternatives.

The results suggest that the G. feliceps spawner biomass has been depleted beyond the recommended (0.5K) level (Fig. 67), an indication of growth-overfishing (Pitcher & Hart 1982). Both sexes are fished close to the critical level of 0.2K, below which recruitment is believed to be detrimentally affected in r-selected fish stocks (Clark et al. 1985). This is an indication that G. feliceps is fairly heavily exploited. Figure 69 indicates that they are also being exploited above $F_{0.1}$, which is used as a management guideline when the yield-per-recruit curve is asymptotic. This is a fairly conservative strategy since it is always lower than the F_{MSY} value. Hughes (1986) mentions, however, that since the yield-per-recruit

model assumes recruitment to be independent of spawner biomass (which it is not), the $F_{0.1}$ management strategy should be adopted since it has a smaller risk factor attached to it. This is particularly important when modeling strongly K-selected species in which recruitment is likely to be strongly dependent upon spawner biomass.

The G. ater population appears to be in a healthy condition in terms of spawner biomass-per-recruit and yield-per-recruit, although the females are slightly more heavily exploited than the males (Figs. 68 & 70).

In the estimation of yield-per-recruit, the model determines the trade-off between the rate of increase in mass of individual fish against the decline in numbers of fish available to the fishery as a result of natural mortality (Butterworth et al. 1989). Since the growth rate of fish is generally fastest during the juvenile phase and since the younger cohorts contain greater numbers of individuals, the yield-per-recruit model will tend to predict higher sustainable yields at relatively young recruitment ages (t_c). When natural mortality is high it is especially advantageous to harvest fish at an early age, and the model demonstrated this in Figure 66 for G. ater males and females. The model predicts that maximum sustainable yields (MSY) will be realised at low t_c values, and that the t_c should decrease as M increases. Since M is higher for males than it is for females, a lower t_c is recommended for males (± 2 years for males and ± 4 years for females). As fishing intensity and thus fishing mortality (F) increases, the model will compensate by increasing (t_c) in order to prevent recruitment overfishing. For G. feliceps F was relatively high and the model estimate of t_c is therefore also set at a proportionately higher value (± 7 years for females and ± 6 years for males), (Fig. 65).

The yield-per-recruit models were originally designed to assess highly r-selected stocks, in which egg and larval mortality has

been shown to be density-dependent (Cushing 1988). This means that even for a fairly small spawner biomass, recruitment is likely to be more-or-less constant from one year to the next. In strongly K-selected species, however, recruitment is more intimately linked with spawner biomass and fluctuations in the latter will probably significantly affect the former. A weakness of the yield-per-recruit model for assessing K-selected populations is, therefore, its failure to consider fecundity as a significant parameter.

The literature has provided abundant proof that excessive depletion of the spawner stock invariably leads to a considerable and rapid decline in catches of K-selected species. Examples include trawl fisheries for mouth-brooding cichlids in the African Great Lakes (Fryer 1984, Witte & Goudswaard 1985, Ribbink 1987), several elasmobranch fisheries (Holden 1977; Compagno In Press), and the fisheries for marine mammals (Allen & Kirkwood 1988).

Although ariids support active artisinal and shallow water commercial fisheries throughout the tropical and subtropical seas, information in the literature relating catch and effort trends are sparse. There is some evidence to suggest that fisheries for barbel stocks using gill nets and trawlers have resulted in unacceptably high mortality rates (Cortés 1984, Pauly & Thia-Eng 1988). Silas et al. (1980) report that purse seine vessels off the coast of Goa are able to identify and target on aggregations of mouth-brooding Tachysurus maculatus (Ariidae). In one month, vessels landed an estimated 528 tons of adults and 38 tons of embryos, a potentially disastrous fishing strategy. Dmitrenko (1970) reported similar activities in the Arabian Sea where spawning aggregations of the ariid Arius thalassinus are actively sought out and trawled for.

It is clearly evident that protection of the spawner biomass should be a priority in fisheries directed at species with low fecundity. In the management of the G. feliceps population the

age at first capture (t_c) should, therefore, be set at above 8 years, corresponding to the approximate age at 50% sexual maturity.

Although the sex ratios for mature G. feliceps indicate that significantly more females are caught in the fishery, this is not the case when juvenile fish are also considered (Table XXVII). However, as approximately 71% of the catch is comprised of mature fish there is a danger that females are being exploited too heavily. It may, therefore, become necessary to impose a closed season for G. feliceps during the spawning season. This would effectively guard against excessive catches of females.

While 97% of the G. ater catch is made up of mature fish, the off season sex ratio does not differ significantly from unity and indicates that the sexes are more equally exploited.

As the two species do not appear to suffer from barotrauma on being caught, probably a result of their phisostomous swim bladders, they lend themselves to the implementation of size limits as a management strategy. When fishes having phisoclistous swim bladders are hauled rapidly to the surface the expansion of air in the swimbladder commonly results in the stomach being everted and blown out through the mouth, and the intestine through the anus. Severe eye embolisms may also occur (Buxton 1987). Practical experience has shown that barbel may be returned to the sea after capture with a high degree of success provided they have not been hooked in or through the stomach or gills. Since barbel may be reproductively active for a period of 7 years or more after reaching sexual maturity, protection of the spawner stock would yield considerable returns in terms of future recruitment.

The spawner stock could be protected using either minimum or maximum size limits. For G. feliceps the size at 50% sexual maturity data (Figs. 14 & 15), indicate that a minimum size

limit of approximately 320-330mm (FL) would provide a degree of spawner protection to both sexes. However, the length-frequency histograms (Figs. 59a & 60a) indicate that the above minimum size limit would effectively exclude approximately 42% of the presently harvested biomass from the fishery. On the other hand, the imposition of this size limit would serve the dual purpose of reducing fishing effort and protecting the spawner biomass.

The imposition of a maximum size limit at approximately 300-310mm (FL) would also have a major effect on the fishery. Although it would offer complete protection to the spawner stock it would exclude approximately 86% of the presently exploited biomass from the fishery. A considerable reduction in the present t_c would then be required in order to realise previous yields. However, evidence suggests that the younger age-classes are more abundant in shallower areas, which explains their poor representation in present catches. Fishing boats tend to avoid areas shallower than approximately 30 meters due to the abundance of small "nuisance" species at these depths such as Boopsoidea inornata, Spondyliosoma emarginatum (Sparidae) and Pomadasys olivaceum (Haemulidae). The imposition of minimum size limits as a management strategy for G. feliceps would therefore be more practical for the fishery, and certainly more acceptable to fishermen. It should be noted that most barbel presently caught in the fishery are clubbed "senseless" by fishermen before being boated. This is to reduce the danger of injury from the poisonous pectoral and dorsal spines. The effectiveness of size limits as a management alternative for barbel would therefore depend on whether or not fishermen could be persuaded to refrain from the above practice.

Barbel have large, bony heads, a stout pectoral girdle and heavy pectoral and dorsal spines, which together comprise a considerable proportion of their body mass. Since fish whole-salers will purchase only the 'head-off gutted weight', the

marketable mass of G. feliceps is a mere 40% of the total body mass. This results in an average marketable mass of approximately 190g and 204g for males and females respectively. The present target species in the commercial fishery are purchased whole (gutted and gilled only), and have the following mean body weights:

kob (Argyrosomus hololepidotus, Sciaenidae) - 1411g,
silver (Argyrozona argyrozona, Sparidae) - 594g,
panga (Pterogymnus laniarius, Sparidae) - 447g.

It is evident that in comparison with the above species, barbel are poor candidates for commercial exploitation.

To summarise, the models indicate that while the G. ater population shows no ill effects from exploitation, G. feliceps is presently being over-exploited. While the yield-per-recruit models indicate that higher sustainable yields would be realised if the ages at first capture were reduced it was argued that the imposition of minimum size limits, set above the size at sexual maturity, would be a more suitable management strategy. As the spawner biomass for G. feliceps was shown to be unacceptably low, protection of the spawner stock was considered to be a priority. It was shown that females were more heavily exploited than males, and it was suggested that a closed season during the spawning and mouth-brooding period would be an effective way of preventing excessive catches of the former. The study demonstrated a sensitivity for G. feliceps to fairly low levels of exploitation.

CHAPTER 7 - GENERAL DISCUSSION

During the course of the study several phenomena were encountered which could not be adequately explained using the data at hand. Examples include the reproductive function of the hyaline eggs, the purpose of the seasonal accumulation of tissue on the pectoral spines of G. ater females, and the functional significance of the sexually dimorphic cleithra in both species. Other potentially rewarding avenues for future investigation are the nature of courtship and spawning behaviour, the extent of sound communication during courtship, the possible utilisation of sneaking as an alternative reproductive tactic in males, the cause of the strongly bimodal length-frequency distribution for the sexes in G. ater, and the degree of interaction between the species at the interphase between reefs and sand, with the premise that one of the two environments is preferred by both species. It would also be interesting to determine whether or not the buccal cavity is an oxygen-poor environment during mouth-brooding, and the value of yolk carotenoids as an endogenous oxygen supply for embryos. Finally, an investigation into the natural mortality rates for the younger age-classes would provide a means of assessing the degree to which the extended parental care behaviour confers a survival advantage on the young.

A study of the biology of Galeichthys feliceps and G. ater initiated with the information contained in the preceding chapters in hand would have enabled more challenging and penetrative investigations to be conducted. However, the establishment of fisheries management policies for the South African linefish stocks, which are diverse and of which relatively little is known, requires the type of base-line biological information that this study has attempted to provide.

In the following pages aspects of the reproduction in G. feliceps and G. ater, particularly their mouth-brooding behaviour, will be discussed. The role of the two species in the Port Alfred commercial linefishery will also be debated in the light of their K-selected life-history traits.

Reproduction

The attainment of an optimal life-history strategy is dependent upon the allocation of energy resources amongst maintenance, growth and reproduction (Gadgil & Bossert 1970), in order to produce a phenotype which realises the highest rate of increase in population size under the given conditions of the environment they inhabit (Reznick 1985). Environmental factors (food and space availability; predators; disease) will be the major determinant of natural mortality in K-selected species, whereas in r-selected species mortality is predominantly density dependent. The criterion for success in natural selection is the number of surviving offspring produced by a parent (Crow & Kimura 1970 in Adams 1980) and the best reproductive strategy is a compromise between two conflicting demands: production of the largest possible number of offspring (r-selection), and production of offspring with the highest possible fitness (K-selection) (Pianka 1970, 1972). A larger allocation of resources to reproduction at any one age leads to better reproductive performance and is interpreted as a profit function. However, there will be a resultant decrease in subsequent growth, survival and reproductive contribution, which is considered a cost function. Natural selection tends to adjust the reproductive effort as an animal ages so that the overall fitness of the life-history is maximised (Williams 1966; Gadgil & Bossert 1970). The cost of reproduction is defined as the trade off between the amount of energy invested in reproduction (fecundity and parental care) and the consequent reduction in growth rate, longevity or capacity for subsequent reproduction (Reznick 1985).

Both Galeichthys species mature at an advanced age and at a proportionately large size when their growth rate and scope for growth (Brett 1979) are considerably reduced and the amount of energy required for maintenance of growth is low. There is a definite switch at the age of sexual maturity from a growth phase to a reproductive phase, particularly amongst males. The decline in growth rate after sexual maturity exhibited by Galeichthys males and their shorter average life-span is suggestive of a higher reproductive investment relative to that of females. In addition, the marked size-frequency dimorphism exhibited by G. ater, males being the smaller sex, indicates that the cost of reproduction for males in this species may be higher than it is in G. feliceps. A comparison of their relative reproductive investment could be used to demonstrate whether mouth-brooding is more expensive for G. ater than it is for G. feliceps males. If it is not, the disparity in growth rate and longevity between the sexes in G. ater is likely to be genetically based.

An interesting phenomenon in Galeichthys reproduction is the way in which resources are allocated to growth and reproduction in the sexes. Both species have a reproductive life-span of approximately nine years. Optimal life-history theory dictates that under these circumstances resources should be allocated equitably between reproductive and non-reproductive activities (Gadgil & Bossert 1970). While this appears to be the strategy employed by females, males tend to invest larger amounts of energy into reproduction at the expense of future growth and survival. Since fecundity does not increase as a function of size in Galeichthys females, the only reproductive advantage to be gained from being large is in mate or territory acquisition. It may be that in Galeichthys it is the females which hold territories or compete for mates and the males which select mates. This role-reversal has been demonstrated in several fish species (Turner 1986; Svensson 1988). The larger average female size would support such an argument. Males lose approximately 28% of their total body weight during the $4^1/_2$-

month mouth-brooding period and contribute approximately $^{1}/_{3}$ more energy to reproduction than females (see Table X). Following mouth-brooding a recovery period of approximately three months is required before they regain their pre-spawning condition. As $7^{1}/_{2}$ months of each year are devoted either directly or indirectly to reproduction, males would appear to have little excess energy available for establishing and defending territories, or for other energetically demanding courtship-related activities.

Species in which one of the sexes assumes the role of parental care invariably utilise courtship rituals to assess the fitness and preparedness of their prospective mates, a phenomenon often referred to as sexual selection (Emlen & Oring 1977; Otte 1979; Baylis 1981; Barnard 1983; Turner 1986; Chan 1987), and it is therefore likely that some form of courtship is employed by Galeichthys.

Since it is the males that care for the young and since each male is able to care for one brood only, kinship theory would have it that in order to make the energy expenditure worthwhile, they should be absolutely sure of their parentage over the incubated brood (see Werren et al. 1980 for review, also Baylis 1981). In contradiction to this argument there was evidence which suggested that sneaking behaviour occurred as an alternative reproductive strategy in a proportion of the male population of both species (the absence of fat reserves in males with ripe testes). Sneaking in fish has been documented for several nest-building species (Werren et al. 1980; Gross 1982, 1984; Turner 1986; Chan 1987), although the construction of nests, the holding of territories or the division of the male population into dominant and sub-dominant individuals may not be pre-requisites for this tactic to be employed. It could conceivably be effective in any situation in which at least some courtship between pairs was involved.

Gross (1984) argued that sneaking might be an evolutionarily stable strategy in one of two ways: either as a subordinate tactic which enabled individuals to make the best of a bad situation (e.g. because they were unable to secure a territory), or as an equivalent tactic in which case their success should decrease as sneaker frequency increased. The latter situation would theoretically enable an equilibrium to exist between sneakers and conventional parents and is probably the more likely of the two scenarios. It is also possible that sneaking frequency may be controlled by a genotype-environmental interaction (Gross op cit). The alleged sneakers in Galeichthys were not noticeably smaller than parental males. This would imply that they were not simply first-time spawners which had been unable to accumulate fat reserves in time for the spawning season. If fishing has created an imbalance in the population sex ratios and females are in short supply, sneaking may be the only way in which a proportion of the male population may hope to achieve fertilisation.

Mouth-brooding

The progressive increase in reproductive specialisation demonstrated within the mouth-brooding guild is largely manifest in the apportionment of increasingly dense yolk into fewer, larger ova (Balon 1981c, 1989; Blumer 1982). This phenomenon appears to have arisen in response to the survival advantage gained by increasing the size of offspring at the culmination of parental care (Oppenheimer 1970; Zale 1987; Balon In Press). Since egg size is positively correlated with development time (Ware 1975) mouth-brooding may have evolved in order to provide a safe environment for the embryo during the extended development period. The most advanced form of mouth-brooding appears to be that exhibited by the cichlid Cyphotilapia frontosa, in which free-embryos are fed within the buccal cavity, harboured until yolk absorption is complete, and released to fend for themselves for the first time as juveniles (Balon op cit.). This is also the category into which the ariids fall. The yolk density of ripe G. feliceps ova is lower

than that occurring in C. frontosa which also has a far higher concentration of lipids, although G. feliceps yolk has a higher protein concentration (Table XXIX). These figures indicate that while C. frontosa yolk has a far higher energy content due to its high lipid fraction, it has a smaller average brood size (17 vs. 49 per clutch) and a far shorter incubation period than G. feliceps (54 vs. 140 days). The average egg size and the size of the young at release, expressed as a percentage of parent size, is 2.8% and 10.7% in C. frontosa and 3.7% and 13.5% in G. feliceps. The increase in size between hatching (onset of exogenous feeding), and release is 48% in C. frontosa and 63% in G. feliceps. The two species therefore have quite different strategies of energy investment. In the cichlid, emphasis has been placed on the production of small clutches of eggs with high energy yolk resulting in rapid development and a short incubation period. G. feliceps has larger egg clutches, lower-energy high-protein yolks and a longer incubation period. Since C. frontosa yolk has a relatively low protein content much of the protein needed for growth appears to be derived through intra-buccal feeding and coeval sibling cannibalism (*sensu* Hecht & Appelbaum 1988). Hatching occurs early in this species, after five to six days (Balon op cit.).

Table XXIX. Proximal yolk composition of the cichlid Cyphotilapia frontosa and the ariid G. feliceps.

	MOISTURE	LIPIDS	PROTEINS	REFERENCE
C. frontosa	44%	35%	20%	Balon (In Press)
G. feliceps	55%	7%	29%	Marais & Venter (1987)

Mouth-brooding has been classified as a low-cost strategy in fish (Mrowka & Schierwater 1988), which capitalises on energy investments made during the preceding non-reproductive, feeding phase. The mouth-brooding adult generally ceases feeding activity, moves into a sheltered environment and becomes highly inactive. Energy expenditure is restricted and geared mainly towards churning of the eggs and the maintenance of an increased ventilation rate until hatching. Mrowka & Schierwater (op cit.) found that non-brooding, feeding individuals had a significantly higher metabolic rate than brooding or starved individuals. In the present study the significant difference in ventilation rates exhibited by non-brooding, feeding males as opposed to males carrying free-embryos is probably also indicative of a sharp decline in adult metabolic rate during mouth-brooding (see Figure 47). The high ventilation rate in adults carrying embryos, on the other hand, is probably necessary to compensate for the inefficient method of embryonic ventilation (oxygen diffusion across the 25µm-thick egg envelope) (Fry 1957). After hatching and the onset of branchial respiration in free-embryos, oxygen assimilation is more efficient and a lower rate of water turn-over is required. It is conceivable that the energy saved in the evolution from substrate guarding (in which considerable energy is expended by the adult in ventilating and protecting broods), to mouth-brooding is redirected into larger eggs and yolk of a higher density.

Evolution of mouth-brooding.

The evolution of parental care in fishes has been discussed by several authors (Werren et al. 1980; Baylis 1981; Gross & Sargent 1985; Sargent & Gross 1986) and in most species it is the male which performs this task (Oppenheimer 1970; Blumer 1982). The opinions expressed in the literature are unanimously in favour of substratum brooding having been the common precursor to mouth-brooding in all species (Iles & Holden 1969; Breder 1933, Myers 1939 in Oppenheimer 1970; Lowe 1959 in

Thys van den Audenaerde 1970; Thys van den Audenaerde 1970; Balon 1975a, 1977, 1984; Baylis 1981; Mrowka 1984).

As male reproductive output is not limited by their rate of gamete production they should, in accordance with Game Theory (Maynard Smith 1977), try and mate with as many females as possible. This is most effectively achieved by defending territories that include favourable spawning sites, a factor which incidentally predisposes them to the evolution of parental care at no extra cost. Females on the other hand should select the fittest males and not engage in parental care. This is because female fecundity generally increases with accelerating returns as body size increases, and they stand to lose more in terms of future reproductive output through loss of body growth, than males (Sargent & Gross 1986). Mouth-brooding probably evolved from monogamous substratum spawners in which there was division of labour between the sexes. This certainly appears to have been the case in the African cichlids in which all species currently exhibiting substratum guarding are strictly monogamous, at least for the duration of one complete breeding cycle (Fryer & Iles 1972). Apogonids are an exception and males may simultaneously incubate the eggs from several females (Thresher 1984). In the evolution of mouth-brooding the sex that was the active guarder would probably also assume the role of buccal incubation, and mouth-brooders may be either male, female, or bi-parental (Baylis 1981).

Buccal incubation is comparatively rare in fishes and has been reported to definitely occur in only seven teleost families (Apogonidae, Ariidae, Belontiidae, Cichlidae, Cyclopteridae, Opisthognathidae and Osteoglossidae) all of which demonstrate male care, although females also brood in three of the families. Gill chamber incubation occurs within the family Amblyopsidae in which females are reported to carry the eggs, although this is not mouth-brooding in the true sense of the word. Luciocephalids (Oppenheimer 1970; Blumer 1982) and malapterurids (Blumer op cit.) are also reported to mouth-brood

although it has yet to be substantiated in these families (Breder & Rosen 1966). Mouth-brooding is therefore predominantly a male trait (Baylis 1981).

Mouth-brooding behaviour has been extensively studied only in the apogonids, ariids and cichlids. All three are highly speciose families and while the apogonids and ariids are primarily marine, cichlids occur almost exclusively in fresh water. In all ariids mouth-brooding is paternal while in apogonids it is predominantly paternal with bi-parental care occurring in four species (Breder & Rosen 1966; Thresher 1984). Amongst the African cichlids it is largely maternal with paternal mouth-brooding occurring in only three tilapia species (Lowe 1959 in Breder & Rosen 1966; Thys van den Audenaerde 1970). Bi-parental mouth-brooding occurs in four species, also tilapines (Iles & Holden 1969). While bi-parental and paternal mouth-brooders are generally monogamous (Lowe 1959 in Breder & Rosen 1966; Fryer & Iles 1972), maternal mouth-brooding cichlid species are generally polygamous and exhibit both polygyny and polyandry.

Since male gametes are energetically inexpensive to produce, males stand to lose far less if their gametes are unsuccessful than do females. In a situation of bi-parental or female mouth-brooding the male might therefore be inclined to abandon the role of parental care in favour of seeking out additional females with which to mate. This would explain the relative paucity of bi-parental mouth-brooders and the prevalence of polygyny amongst cichlid maternal mouth-brooders. Maternal bearing is considered to be evolutionarily the most stable while bi-parental and paternal mouth-brooding are considered unstable (Gross & Sargent 1985).

In some apogonids, eggs of a relatively small size (0.4mm) have been retained enabling many hundreds and even thousands to be incubated simultaneously by the male, often from several different females (Thresher 1984). In this polygynous situation

male mouth-brooding may be evolutionarily more stable. Amongst the ariids, in which few eggs are produced and in which paternal care is prolonged, male reproductive output is very limited and mouth-brooding is expected to be evolutionarily unstable. In producing such large eggs requiring extended development periods, females may have effectively 'coerced' the males into enduring longer and longer periods of mouth-brooding (sensu Gross & Sargent 1985). It is unlikely that an evolutionary trend toward fewer, larger eggs will continue much further in ariids because a point in the duration of mouth-brooding will eventually be reached beyond which males will not be able to survive. It would appear that Galeichthys males are already energetically over-extended during the incubation period (see pp.204-205) and have probably reached a state of "reproductive recklessness" (*sensu* Calow 1979) with respect to their costs of reproduction.

In the light of the concomitant restriction of male reproductive output associated with monogamous paternal mouth-brooding its prevalence amongst teleosts is surprising. Baylis (1981) argues that monogamous male care may be stable because increased survivorship of young offsets their reduced primary fecundity. In addition, he argues that solitary male or female care would have evolved only if it imparted maximum and equal reproductive advantage on both sexes. This implies that maximum reproductive success will have been achieved in Galeichthys when any one brood is fertilised and successfully reared in one breeding season, and males should therefore have no inclination to fertilise additional broods.

The barbel fishery - Implications of K-selection

The K-selected traits of G. feliceps and G. ater which are of relevance to their management are presented in Table XXX.

Table XXX. The K-selected life-history traits of G. feliceps and G. ater.

Life-history traits	G. FELICEPS		G. ATER	
	Males	Females	Males	Females
Age at 50% maturity (Yrs)	9.8	8.9	8.8	7.4
Maximum age (Yrs)	>16	>18	>15	>15
Growth rate (K)	0.147	0.120	0.193	0.132
Natural mortality rate (M)	0.137	0.101	0.211	0.133
Mean Fecundity		49.3		31.5
Mouth-brooding duration (Days)	±140		?	

While most r-selected species have high fecundities and density-dependent mortality of egg and larval stages (Cushing 1988), K-selected species have low fecundity, density-independent pre-recruit mortality (Adams 1980) and a small population compensatory capacity, or 'scope for compensation' (Garrod & Horwood 1984). Rather than producing a surplus of young they have adopted physiological and behavioural devices to overcome the vulnerability of their early life-history stages.

A primary contributing factor to their population stability appears to be their consistently high recruit survival from one year to the next (i.e. low natural mortality). Garrod & Horwood (1984), in their particle size theory, suggest that natural mortality is essentially a reflection of the relative abundance of particles of different sizes in the environment (either predator or prey) and that the trajectory of natural mortality is common to all species of equal size in an ecosystem. This implies that although precocial species care for their young

until they are of a large size they will be as vulnerable as any other organism of similar size once they are released to fend for themselves. By delaying the point of entry into the general mortality trajectory precocial species provide protection during the most vulnerable ontogenetic stages. The larger the young when released, the fewer predators there will be that are large enough to eat them. Sissenwine (1984) stated that predation was probably the major cause of natural mortality in fish. If this assumption, and the particle size theory of Garrod & Horwood (1984) are accepted, large body size would confer a considerable survival advantage on an individual. Galeichthys are able to use their erectable pectoral and dorsal spines to simulate this, a trait which effectively compensates for their comparatively slow growth rate. In addition, although they are prey to a wide variety of animals including fish, sharks, rays, seals and birds, their defensive weaponry is likely to render them less attractive as a food source throughout their life-cycle than other species of equable body size. This phenomenon was experimentally demonstrated by Hoogland et al. (1957 in Barnard 1983) who found that pike (Esox lucius), when provided with minnows, ten-spined sticklebacks and three-spined sticklebacks, fed selectively, first on the minnows, then the ten-spined sticklebacks and lastly on the three-spined sticklebacks, which have large, locking spines.

As K-selected species are generally highly competitive their populations are stable (Pianka 1970) and if managed properly, should theoretically be able to support sustained harvests in the long term (Adams 1980). However, Holden (1974, 1977) has shown that stocks of several elasmobranchs which form by-catches in trawl fisheries for more fecund teleosts in the North Atlantic and in the North Sea, have crashed. Holden (op cit.) attributed these population declines to their low reproductive potential and lack of reproductive flexibility with respect to both the age at sexual maturity and fecundity. A major problem associated with these trawl fisheries was that

elasmobranch-directed effort could not be reduced even after it had become apparent that the populations were in a decline. While it would be possible to impose effort restrictions on barbel catches in the Port Alfred fishery, this study has shown that Galeichthys are sensitive to even mild exploitation and it is questionable whether they could be profitably exploited at the low levels of effort required to ensure their long-term survival.

As a consequence of their low fecundity, recruitment in K-selected populations is directly related to spawner biomass and inversely proportional to the number of spawners harvested (Holden 1974, 1977). As the yield-per-recruit models assume that recruitment is independent of spawner biomass they are inappropriate for use with K-selected populations (Holden op cit.). A more appropriate method used by Holden & Meadows (1964 in Holden 1977) for elasmobranch populations utilises growth rate, age at sexual maturity for female fish, brood size, the sex ratio of the young and the duration of the breeding cycle to determine the number of female young that an initial cohort of females (e.g. 1000 individuals) could produce under the prevailing total mortality rate for the stock. If the hypothetical female cohort is unable to replace itself during its lifetime then fishing effort is too high. As an exercise, the G. feliceps data were applied to this model and yielded results which varied widely depending on the natural mortality rate used. As the natural mortality rate in a cohort is highest at the smallest sizes and decreases with increasing size it is meaningless to use a single value of M for all ages in the calculations. Using the three different values of M (0.078, 0.101, and 0.126) which were used in the Beverton-Holt spawner biomass-per-recruit and yield-per-recruit models the model produced the following results: for an initial cohort of 1000 females the model predicted that at the age of 18 years approximately 51 016, 40 758 and 32 957 female offspring would have been produced for the three values of M respectively. The above methodology is presented in Appendix IV. These figures

indicate that at the present total mortality rate G. feliceps cohorts would more than replace themselves during their lifetime. This result suggests that the stock is not over-exploited, and it is contrary to the results of the Beverton-Holt spawner biomass-per-recruit models which indicated that the spawner biomass has declined considerably. It is interesting to note that although the Beverton-Holt model is thought to be inappropriate for use with K-selected species it provided more conservative results for the G. feliceps female population than the model of Holden & Meadows (op cit.) above.

Multi-species management approaches are generally considered preferable to the independent modeling of single species (Gulland & Garcia 1984) although this argument applies more strongly to trawl fisheries than it does to linefisheries. Species-specific management regulations such as size limits, bag limits and closed seasons are effectively employed in linefisheries and allow a high degree of control over fishing mortality (Smale & Buxton 1985; Van der Elst 1985; Bennett & Griffiths 1986; Buxton 1987; Huntsman & Waters 1987; Griffiths 1988; Hecht & Tilney 1989). This is particularly true for ariids which are seemingly unaffected by barotrauma and can be successfully returned to the water after capture. Several management alternatives are therefore open for the regulation of the Port Alfred barbel fishery.

The spawner biomass-per-recruit and yield-per-recruit vs. fishing effort curves demonstrated that the G. ater stock has not been adversely affected by present levels of fishing effort. The following discussion is thus directed at the G. feliceps stock.

While the study has shown that G. feliceps may be over-exploited the imposition of restrictive regulations in the fishery at present are likely to be unpopular. This is because barbel currently have little commercial value and are regarded

largely as a "nuisance" in the fishery. The danger in not taking management action now lies in the difficulty of detecting the critical point beyond which imminent stock collapse will occur. As barbel are slow maturing and since predominantly mature fish are caught in the fishery recruitment failure will not be detected until several years after the event when it may be too late to rectify the damage. When K-selected stocks collapse, recovery is slow and seldom complete because once their numbers have been cropped below the level at which they are able to occupy their spacial and foraging niches, these are rapidly filled by opportunistic, altricial species which are highly successful colonisers (Hsu 1982 in Bruton 1989).

An important point for consideration in the interpretation of yield-per-recruit and spawner biomass-per-recruit curves in this study was that a large percentage of the adult males were excluded from the catches for a period of approximately four months each year while mouth-brooding. The sex ratio and population structure reflected in the catches may not have been a true representation of the population structure in the ocean and the catch-curves used will have yielded mortality values for males which were over-estimates.

However, the sex ratios did indicate that catches during the spawning and mouth-brooding period significantly favoured females (female:male ratio = 1.65:1 and 2.23:1 for G. feliceps and G. ater respectively, see Table XXVII), suggesting that some sort of effort restriction should be imposed to reduce barbel catches during this period. Restrictions in the form of a closed season, bag limits or size limits would all prove effective.

Given the fact that barbel are caught in association with kob, their catches are directly influenced by the amount of effort that is directed at the latter. In recent years there has been a decline in kob-directed effort in the Port Alfred fishery

(Hecht & Tilney 1989) and barbel are experiencing a temporary reprieve from previous, higher levels of exploitation. Kob formed the major component of the total annual landings in the fishery between the 1960's and the mid 1980's. In 1987 kob catches were surpassed for the first time by those of two sparids Argyrozona argyrozona and Pterogymnus laniarius, which are caught in deeper water (Hecht & Tilney op cit.). The imposition of restrictions on barbel catches at this stage may therefore be premature. As barbel form an important source of revenue and protein for the largely impoverished fishermen who catch them, there is a socio-economic consideration which also weighs against the imposition of catch restrictions at present. Should increasing market prices result in barbel exploitation becoming profitable it will be necessary to re-assess the stocks before arriving at a suitable management strategy. The differential exploitation of the sexes is seen as an important area for regulation. Protection of the spawner biomass would also be a priority and could be achieved using minimum size limits set at a fork length of approximately 320-330mm. However, as this would exclude a large proportion of the stock presently available to the fishery, it may prove unacceptable to fishermen. The most effective strategy would therefore be to impose a closed season during the mouth-brooding period between September and December. This would limit effort, protect the population sex ratio, and have the added advantage of being easy to control.

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APPENDIX I

Stomach content analyses

Appendix Ia:

G. FELICEPS: MARINE	%NO	WT	% ENERGY	%F.O.	E.I.
CRUSTACEA TOTAL	65.67	350.70		84.01	
AMPHIPODA TOTAL	0.44	0.24	0.04	2.03	0.09
Paramoera capensis	0.06	0.02		0.25	
Unidentified	0.38	0.22		1.49	
ANOMURA TOTAL	0.25	5.43	1.30	1.16	1.37
Calianassa kraussi	0.06	3.80	0.91	0.25	0.20
Unidentified	0.19	1.63		0.75	
BRACHYURA TOTAL	42.29	325.13	46.87	61.34	3222.28
Atelecyclus septemdentatus	0.06	1.79		0.25	
Goneplax angulata	14.96	130.73	18.85	18.16	383.58
Hymenosoma orbiculare	1.17	2.52		3.98	
Mursia cristimanus	0.06	0.02		0.25	
Nautilocorystes ocellata	0.45	6.99		1.24	
Ovalipes punctatus	3.82	15.94		2.49	
Philyra punctata	0.97	2.93		1.49	
Thaumastoplax spiralis	16.97	154.51	22.27	25.62	639.66
Unidentified chelae	1.17	6.94		4.23	
Unidentified megalopae	2.66	2.76		6.72	
ISOPODA TOTAL	5.24	5.85	1.04	4.94	5.75
Cirolana meinerti	0.39	0.62		0.50	
Synidotea hirtipes	2.20	2.51		1.99	
Unidentified	2.66	2.72		2.49	
MACRURA TOTAL	3.36	11.42	1.71		
Caridea	3.30	11.28		6.47	12.23
Palinura	0.06	0.14		0.25	
MYSIDACEA					
Unidentified	13.92	2.33	0.22	6.22	1.51
STOMATOPODA					
Lysiosquilla capensis	0.13	0.30		0.50	
ECHIURIDA TOTAL	12.31	153.33	25.97	34.01	989.86
Ochaetostoma capense	9.78	144.07		25.87	
O. capense - proboscis	2.53	9.26		3.98	
MOLLUSCA TOTAL	3.63	10.59		12.21	
CEPHALOPODA		4.73	1.02		
Octopus spp.	0.71	4.50		2.74	2.98
Sepia sp.	0.06	0.23		0.25	
GASTROPODA					
Unidentified	0.65	0.32		1.74	
PELECYPODA		6.19	0.38		
Phaxas decipiens	1.62	5.54	0.34	6.97	2.66
Unidentified	0.58	0.65		2.24	
POLYCHAETA TOTAL	16.69	90.72	20.45	30.52	699.59
ERRANTIA Total	5.10	32.01	7.22	14.43	116.71
Diopatra cuprea	0.06	0.43		0.25	
Glycera convoluta	0.26	0.86		0.25	
Marphysa macintoshi	0.06	3.74		0.25	
Trypanosyllis gemmullfera	0.32	6.10		0.25	
Unidentified	4.40	20.88		14.43	
SEDENTARIA Total	11.59	58.71	13.24		
Pherussa sp.	0.58	1.31		0.75	
Sternaspsis scutata	10.30	52.76	11.89	12.19	121.87
Unidentified	0.71	4.64		2.49	
SIPUNCULIDA					
Unidentified	0.06	0.31		0.25	

Appendix Ia contd.

	%NO	WT	% ENERGY	%F.O.	E.I.
SPERMATOPHYTA					
Unidentified detritus	0.13	0.58			
TELEOSTEI TOTAL	1.55	5.44		4.36	5.08
Scales	0.91	0.14		1.49	
Unidentified	0.65	5.30	1.01	2.24	2.53
CRUSTACEAN REMAINS		32.06		25.00	
UNIDENTIFIED REMAINS		34.06		10.76	

STOMACH NUMBER	402
EMPTY STOMACH NUMBER	58
SIZE RANGE (F.L.)	232-360mm
MAXIMUM STOMACH INDEX	4.01%

Appendix Ib:

G.ATER: MARINE	%NO	WT	% ENERGY	%F.O.	E.I.
ALGAE					
Unidentified		0.22		1.18	
BRYOZOA					
Unidentified		0.59		3.14	
CRUSTACEA					
ANOMURA TOTAL	1.99	11.47	3.79	6.06	22.97
Galathea dispersa	1.19	10.19	3.37	3.53	11.89
Unidentified	0.80	1.28		2.53	
BRACHYURA TOTAL	17.92	92.19	33.83	40.78	1379.72
Atelecyclus septemdentatus	0.69	7.35	2.43	1.96	4.76
Cryptodromiopsis spongiosa	0.30	1.77		1.09	
Dehaanius dentatus	1.59	9.97	3.29	5.10	16.80
Dromidiopsis cornuta	0.30	1.53		0.72	
Goneplax angulata	0.50	2.65		1.45	
Hymenosoma orbiculare	0.69	0.68		1.81	
Matuta sp.	0.30	1.11		1.09	
Macropodia falcifera	0.69	2.08		2.54	
M. formosa	0.50	2.60		0.36	
Parapilumnus pisifer	0.30	1.83		1.09	
Philyra punctata	0.20	0.55		0.36	
Plagusia chabrus	1.29	19.33	6.39	4.31	27.56
P. chabrus - megalopae	4.16	5.15		6.52	
Portumnus biguttatus	0.10	2.40		0.36	
Unidentified chelae	1.59	3.98		3.62	
Unidentified crabs	9.58	23.92		15.58	
ISOPODA TOTAL	17.84	29.75	12.10	42.35	512.64
Antarcturus kladophorous	0.10	0.10		0.36	
Arcturella corniger	0.50	0.40		1.45	
Cirolana sp.	0.50	0.25		1.09	
Cymodoce amplifrons	0.79	3.26		2.17	
C. comans	0.30	0.65		0.36	
C. tetrathele	0.10	0.32		0.36	
C. umbonata	0.10	0.68		0.36	
C. uncinata	0.99	1.35		2.17	
C. valida	3.96	9.74		11.23	
C. velutina	0.30	0.72		1.09	
Cymodocalla sp.	0.50	0.10		0.72	
Exosphaeroma antikraussi	0.10	0.57		0.72	
Exosphaeroma sp.	0.20	0.01		0.36	
Haliophasma foveolata	0.99	1.23		1.81	
Idotea metallica	0.10	0.04		0.36	
Neastacilla tranquilla	0.20	0.03		0.72	
Panathura sp.	0.10	0.02		0.36	
Paraciliacea sp.	0.20	0.57		0.72	
Rocinela granulosa	0.20	0.12		0.72	
Synidotea hirtipes	0.10	0.16		0.36	
S. setifer	0.10	0.36		0.36	
S. variegata	0.10	0.01		0.36	
Unidentified	7.33	9.03		17.03	
MACRURA TOTAL	17.25	12.44	4.27	22.45	95.79
Caridea	16.85	11.29	3.87	22.75	88.08
Penaeida	0.40	1.15		1.45	
PALINURA					
Scyllarus elisabethae	2.12	5.29	1.75	2.75	4.80
ECHINODERMATA					
HOLOTHUROIDEA					
Unidentified	0.40	2.97		1.45	
ECHIURIDA					
Ochaetostoma capense	1.68	15.14	5.88	5.10	29.96
HYDROZOA TOTAL		0.10		0.72	
Gymnangium arcuatum		0.09		0.36	
Sertularella sp.		0.01		0.36	

Appendix Ib contd.

		%NO	WT	% ENERGY	% F.O.	E.I.
MOLLUSCA	TOTAL	6.14	36.17		12.32	
CEPHALOPODA	Total	3.08	30.44	15.04	13.33	200.56
Loligo sp.		0.10	1.00		0.36	
Octopus sp.		2.78	14.57		7.61	
Sepia sp.		0.20	8.70		0.72	
GASTROPODA	Total	2.18	5.97	6.87	6.15	42.27
Fissurella sp.		1.19	5.50	6.33	2.75	17.38
Nassa scopularcus		0.10	0.10		0.36	
Unidentified		0.89	0.37		3.26	
PELECYPODA						
Unidentified		0.89	0.20		3.26	
POLYCHAETA	TOTAL	13.38	29.98	15.49	33.33	516.39
ERRANTIA	Total	11.00	22.91	11.84	33.33	394.65
Eunice sp.		0.10	2.97		0.36	
Euphrosine capensis		0.10	0.05		0.36	
Lysidice natalensis		0.10	0.16		0.36	
Platynereis dumerilli		0.10	0.12		0.36	
Unidentified		10.60	19.61		29.35	
SEDENTARIA	Total	2.38	7.07	3.65	8.23	30.07
Flabelligera affinis		0.10	0.16		0.36	
Pherussa sp.		1.59	3.15		5.07	
Unidentified		0.69	3.76		2.17	
SIPUNCULIDA						
Themiste spp.		0.40	2.26		1.45	
TELEOSTEI	TOTAL	4.26	18.36	8.01	5.88	47.14
GOBIIDAE						
Unidentified		0.30	0.22		1.09	
OPHICHTHYIDAE						
Unidentified		0.10	9.11		1.09	
TELEOST REMAINS		1.29	9.03		4.71	
Scales		2.58	0.22		1.09	
CRUSTACEAN REMAINS			9.07		12.55	
UNIDENTIFIED REMAINS			12.35		11.76	

STOMACH NUMBER	285
EMPTY STOMACH NUMBER	30
SIZE RANGE (F.L.)	195-322mm
MAXIMUM STOMACH INDEX	4.05%

Appendix Ic:

G.FELICEPS: T.B. DAVIE - MARINE	%NO	WT	% ENERGY	%F.O.	E.I.
CRUSTACEA TOTAL	83.92	0.51		95.83	
AMPHIPODA TOTAL	0.30	0.01	0.24	4.17	1.00
Cunicus profundus	0.15	0.01		2.08	
Unidentified	0.15	0.01		4.17	
ANOMURA TOTAL	0.44	0.12	4.02	6.25	25.15
c.f. Clibanarius longitarsus	0.15	0.04		2.08	
Unidentified	0.29	0.08		6.25	
BRACHYURA TOTAL	1.61	0.27	5.59	12.50	69.84
Thaumastoplax spiralis	1.32	0.18	3.69	8.33	30.74
Unidentified chelae	0.29	0.09			
MYSIDACEA TOTAL	79.24	0.11	1.49	52.08	77.52
Mesopodopsis africanus	0.15	0.01		2.08	
Unidentified	79.09	0.11		52.08	
ECHIURIDA					
Ochaetostoma capense	4.68	4.62	76.48	35.42	2708.65
MOLLUSCA					
CEPHALOPODA	0.15	0.12	3.77	2.08	7.85
MUCOUS		1.23	5.85	46.00	268.89
POLYCHAETA					
ERRANTIA	1.75	0.02	0.73	16.67	12.11
TELEOSTEI TOTAL	9.51				
Scales	8.63	0.11	1.85	37.50	69.55
Spines	0.88				
CRUSTACEAN REMAINS		0.01		4.16	
UNIDENTIFIED REMAINS		0.29		35.42	
STOMACH NUMBER 48					
EMPTY STOMACH NUMBER 0					
SIZE RANGE (FL) 47-145mm					

Appendix Id:

G. ATER JUVENILES: SUB-TIDAL GULLY	%NO	WT	%ENERGY	%F.O.	E.I.
CRUSTACEA TOTAL		1.87		100.00	
AMPHIPODA TOTAL		0.88	33.41	97.50	3257.04
Gammaridea		0.85		92.68	
Caprellidea		0.03		24.39	
BRACHYURA					
Unidentified		0.04	1.34	2.44	3.27
ISOPODA TOTAL		0.85	35.18	62.50	2197.42
Cirolana sp.		0.01		2.44	
Cymodocella pustulata		0.01		2.44	
C. sublevis		0.05		7.32	
Dynamenella huttoni		0.01		2.44	
D. ovalis		0.05		2.44	
Exosphaeroma sp.		0.01		2.44	
Gnathia africana		0.02		2.44	
Isocladus otion		0.03		4.88	
Munna sheltoni		0.36		12.20	
Parisocladus perforatus		0.10		9.76	
MACRURA					
Macrobrachium equidens		0.04	1.39	2.44	3.39
OSTRACODA					
Unidentified		0.08	2.72	4.88	13.29
HYDROZOA					
Sertularia sp.		0.01		2.44	
MOLLUSCA					
GASTROPODA					
Oxystele sp.		0.01	1.17	12.50	14.60
MUCOUS		0.31	2.37	36.59	86.59
POLYCHAETA					
ERRANTIA					
Unidentified		0.43	22.49	65.00	1461.60
STOMACH NUMBER 41					
EMPTY STOMACH NUMBER 1					
SIZE RANGE (FL) 61-121mm					

Appendix Ie:

G.FELICEPS: KOWIE RIVER - JUVENILES	%NO.	WT	% ENERGY	%F.O.	E.I.
CRUSTACEA TOTAL	40.84	100.96		89.13	
AMPHIPODA					
Unidentified	0.21	0.01		1.09	
ANOMURA TOTAL	6.43	74.58		43.48	
Callianassa kraussi	0.32	4.40	3.22	3.26	10.50
Upogebia africana	6.11	70.18	72.86	40.22	2930.27
BRACHYURA TOTAL	15.86	22.37		45.65	
Cleistostoma edwardsii	7.82	14.07	7.67	19.57	150.12
Hymenosoma orbiculare	4.61	3.27	1.78	30.43	54.27
Thaumastoplax spiralis	3.00	4.16	2.27	22.83	51.78
Unidentified chelae	0.43	0.87		2.17	
ISOPODA TOTAL	11.36	2.41	1.62	30.43	49.25
Aega spp.	0.64	0.14		3.26	
Cymodose spp.	0.21	0.06		2.17	
C. africana	0.21	0.10		1.09	
Clrolana fluviotilis	0.11	0.05		1.09	
Exosphaeroma antikraussi	0.11	0.05		1.09	
E. hylocoetes	4.07	1.04		11.96	
E. truncatitelson	2.47	0.39		8.70	
Unidentified	3.54	0.58		10.87	
MACRURA TOTAL	1.61	0.72	0.41	9.78	3.99
Macropetasma africanum	0.64	0.60	0.34	3.26	1.11
Unidentified Caridea	0.75	0.09		5.43	
Unidentified Penaeida	0.21	0.03		2.17	
MYSIDACEA TOTAL	5.36	0.87	0.31	6.52	1.99
Mesopodopsis slabberi	3.75	0.37		5.43	
Unidentified	1.61	0.50		1.09	
MOLLUSCA TOTAL	3.22	0.16	0.04	11.96	0.48
GASTROPODA	0.21	0.04		2.17	
PELECYPODA	3.00	0.12		9.78	
POLYCHAETA TOTAL	2.57	0.22	0.19	9.78	1.86
ERRANTIA					
Phyllodose madeirensis	2.14	0.17		5.43	
Unidentified	0.43	0.05		4.35	
SPERMATOPHYTA TOTAL		2.44		8.70	
Detritus		0.01		1.09	
Zostera sp.		2.43	1.89	7.61	14.35
TELEOSTEI TOTAL	52.63	13.22	6.95	35.87	68.00
Atherina breviceps	0.54	0.40		3.26	
Caffrogobius agulhensis	0.11	0.12		1.09	
Liza sp.	0.11	0.18		1.09	
Scales	38.80	2.53	1.10	30.43	33.36
Spines	12.11	1.04		7.61	
Unidentified	0.96	8.95		9.78	
TUNICATA	0.75	0.17		3.26	
CRUSTACEAN REMAINS		5.96		15.22	
UNIDENTIFIED REMS		16.95		9.78	

STOMACH NUMBER	112
EMPTY STOMACH NUMBER	20
MAXIMUM STOMACH INDEX	9.98%
SIZE RANGE (F.L.)	125-215mm

Appendix If:

FISH RIVER: JUVENILES		%NO	WT	%ENERGY	%F.O.	E.I.
CRUSTACEA	TOTAL	66.23	9.91		82.20	
AMPHIPODA						
Unidentified		49.52	1.63	15.88	40.00	635.07
ANOMURA						
Callianassa kraussi		1.03	3.51	40.32	24.44	985.50
Upogebia africana		0.08	0.04	0.65	2.22	1.45
BRACHYURA	TOTAL	2.25	3.59	22.13	33.33	737.74
Cleistostoma edwardsii		0.72	1.00		11.11	
Hymenosoma orbiculare		0.16	0.19		2.22	
Unidentified		1.35	2.39		26.67	
ISOPODA						
Unidentified		0.40	0.02	0.18	8.89	1.61
MACRURA	TOTAL	7.08	0.63	5.60	31.11	174.33
Caridea		0.72	0.15		11.11	
Penaeida		6.36	0.48		20.00	
MYSIDACEA						
Unidentified		5.64	0.34	1.85	17.78	32.86
OSTRACODA						
Unidentified		0.24	0.15		6.67	
POLYCHAETA						
Unidentified		0.08	0.05	0.67	2.22	1.49
TELEOSTEI						
Scales		33.55	1.87	12.72	82.22	1045.53
STOMACH NO	46					
EMPTY STOMACH NO	1					
SIZE RANGE (FL)	45-180mm					

Appendix Ig:

FISH RIVER: MATURE FISH		%NO	WT	% ENERGY	%F.O.	E.I.
CRUSTACEA	TOTAL	95.65	12.99		89.13	
ANOMURA	TOTAL	15.21	9.31	44.00	46.15	2030.77
Callianassa kraussi		13.04	8.33		38.46	
Upogebia africana		2.17	0.98		7.69	
BRACHYURA						
Unidentified		15.22	0.76	3.00	23.08	69.23
MACRURA						
Penaeida		10.87	2.27	8.00	30.77	246.15
MYSIDACEA						
Unidentified		54.35	0.65	1.00	15.38	15.38
SPERMATOPHYTA						
Zostera sp.			0.15		15.38	
TELEOSTEI						
Unidentified		4.35	10.00	44.00	15.38	676.92
UNIDENTIFIED REMAINS			2.31			
STOMACH NO	23					
EMPTY STOMACH NO	10					
SIZE RANGE (FL)	290-400mm					

Appendix Ih:

G.FELICEPS: MTATI RIVER - JUVENILES	%NO	WT	% ENERGY	%F.O.	E.I.
CRUSTACEA TOTAL	9.45	3.44		86.84	
AMPHIPODA					
Unidentified	3.16	0.10	0.37	22.86	8.48
ANOMURA					
Callianassa kraussii	0.12	0.67	2.92	8.57	25.03
BRACHYURA TOTAL	0.49	0.65	2.12	20.00	42.50
Hymenosoma orbiculare	0.12	0.03		2.63	
Unidentified	0.37	0.62		15.79	
ISOPODA					
Unidentified	5.47	2.00	8.06	40.00	322.46
MACRURA					
Caridea	0.20	0.03	0.10	2.63	0.27
MOLLUSCA TOTAL	0.08	0.10		5.26	
GASTROPODA					
Assiminea bifasciata	0.04	1.49		2.63	
PELECYPODA					
Unidentified	0.04	0.01		2.63	
POLYCHAETA					
Unidentified	0.04	0.02	0.10	2.63	0.27
SPERMATOPHYTA					
Zostera sp.		0.14	0.66	22.86	15.12
TELEOSTEI TOTAL	90.43	29.52		100.00	
Caffrogobius multifasciatus	0.08	1.49	6.44	2.63	16.95
Unidentified	0.45	3.79	16.39	28.95	474.49
Scales	89.90	24.25	63.06	100.00	6306.27
UNIDENTIFIED REMAINS		0.69		36.84	

STOMACH NUMBER	38
EMPTY STOMACH NUMBER	3
SIZE RANGE (FL)	175-214mm

Appendix Ii:

G.FELICEPS: FREE EMBRYOS		WT	%WT	%FO
ALGAE				
Unidentified Remains		0.001	1.471	3.704
CRUSTACEA	TOTAL	0.020	29.412	37.037
COPEPODA				
Unidentified		0.008	11.765	14.815
ISOPODA				
Unidentified remains		0.006	8.824	7.407
EXOSKELETA				
Unidentified		0.006	8.824	14.815
HYDROZOA				
Unidentified remains		0.003	4.412	7.407
MOLLUSCA				
GASTROPODA		0.002	2.941	3.704
MUCOUS		0.004	5.882	33.333
PORIFERA				
Spicules		0.001	1.471	3.704
SAND		0.012	17.647	74.074
SPERMATOPHYTA				
Leafy remains		0.011	16.176	66.667
Woody remains		0.009	13.235	33.333
TELEOSTEI				
Unidentified remains		0.003	4.412	3.704
Yolk		0.002	2.941	3.704
STOMACH NO	27			
EMPTY STOMACH NO	0			
SIZE RANGE (FL)	30-49mm			

APPENDIX II

Appendix IIa:

G. FELICEPS: OTOLITH RADIUS AND OTOLITH LENGTH AT SIZE
T-TEST: MALES VS FEMALES

OTOLITH RADIUS

	MALES			FEMALES				
SIZE CLASS	N	MEAN OT. RAD	SD	N	MEAN OT. RAD	SD	t-TEST	df	SIG DIF (Y=*/N=-)
250-259	5	4.32	0.194	3	4.47	0.157	-0.58517	6	-
260-269	5	4.33	0.145	2	4.54	0.127	-0.92278	5	-
270-279	7	4.37	0.146	3	4.48	0.444	-0.27017	8	-
280-289	2	4.87	0.537	1	4.48	0	0.592986	1	-
290-299	9	4.81	0.373	5	4.7	0.319	0.284989	12	-
300-309	9	4.95	0.314	8	4.73	0.244	0.811391	15	-
310-319	7	5.25	0.268	5	5.14	0.31	0.325018	10	-
320-329	11	5.22	0.424	16	5.23	0.506	-0.02745	25	-
330-339	14	5.38	0.576	15	5.36	0.375	0.056592	27	-
340-349	4	6.12	0.527	15	5.82	0.443	0.549602	17	-
350-359	3	5.67	0.612	7	5.79	0.364	-0.17817	8	-
360-369				3	6.31	0.655			

OTOLITH LENGTH

	MALES			FEMALES				
SIZE CLASS	N	MEAN OT. LN.	SD	N	MEAN OT. LN.	SD	t-TEST	df	SIG DIF (Y=*/N=-)
250-259	5	10.1	0.282	3	10.19	0.244	-0.23429	6	-
260-269	5	10.38	0.428	2	9.95	0.071	1.029956	5	-
270-279	7	10.35	0.381	3	10.63	0.693	-0.37780	8	-
280-289	2	10.17	0.092	1	10.02	0	1.331244	1	-
290-299	9	10.86	0.55	5	10.67	0.316	0.393348	12	-
300-309	9	11	0.646	8	11.16	0.383	-0.31999	15	-
310-319	7	11.56	0.446	5	11.65	0.211	-0.23394	10	-
320-329	11	11.82	0.858	16	11.74	0.474	0.153341	25	-
330-339	14	11.99	0.537	15	12.28	0.594	-0.68999	27	-
340-349	4	12.4	0.515	15	12.44	0.562	-0.06599	17	-
350-359	3	12.95	0.545	7	12.75	1.029	0.184134	8	-
360-369				3	12.7	0.46			

Appendix IIa contd.:

G. ATER: MEAN OTOLITH RADIUS AND OTOLITH LENGTH AT SIZE
T-TEST: MALES VS FEMALES

OTOLITH RADIUS

	MALES			FEMALES				
SIZE CLASS	N	MEAN OT. RAD.	SD	N	MEAN OT. RAD.	SD	t-TEST	df	SIG DIF (Y=*/N=-)
220-229	3	4.39	0.354						
230-239	3	4.36	0.417	6	4.31	0.228	0.109628	7	-
240-249	24	4.78	0.37	5	4.58	0.283	0.623029	27	-
250-259	25	4.73	0.316	11	5.04	0.454	-1.11272	34	-
260-269	18	5.07	0.372	9	4.9	0.368	0.562720	25	-
270-279	5	5.3	0.437	27	5.05	0.416	0.601981	30	-
280-289	4	5.2	0.261	21	5.4	0.458	-0.50988	23	-
290-299				18	5.61	0.48			
300-310				9	5.66	0.478			
310-319				4	6.06	0.183			

OTOLITH LENGTH

	MALES			FEMALES				
SIZE CLASS	N	MEAN OT. LN.	SD	N	MEAN OT. LN.	SD	t-TEST	df	SIG DIFF (Y=*/N=-)
220-229	3	9.67	0.494						
230-239	3	10.13	0.748	6	9.91	0.488	0.251720	7	-
240-249	24	10.47	0.579	5	10.51	0.503	-0.07520	27	-
250-259	25	10.85	0.405	11	10.88	0.372	-0.10671	34	-
260-269	18	11.4	0.369	9	11.12	0.509	0.781158	25	-
270-279	5	11.5	0.476	27	11.46	0.584	0.077507	30	-
280-289	4	11.42	0.637	21	11.89	0.54	-0.73196	23	-
290-299				18	12.12	0.539			
300-310				9	12.25	0.402			
310-319				4	12.81	0.389			

Appendix IIa contd.:

G. FELICEPS: MEAN WEIGHT AT SIZE
T-TEST: MALES VS FEMALES

	MALES			FEMALES				
SIZE CLASS	N	MEAN WT	SD	N	MEAN WT	SD	t-TEST	df	SIG DIF (Y=*/N=-)
250-259	16	251.4	18.94	10	238.9	12.83	0.976036	24	-
260-269	15	278	30.71	8	268.9	19.09	0.417386	21	-
270-279	14	314.3	33.83	16	320.3	30.55	-0.25466	28	-
280-289	13	356.2	38.11	16	321.4	26.15	1.450344	27	-
290-299	26	401.5	40.24	27	395	44.55	0.278996	51	-
300-309	21	437.5	35.86	41	426.7	41.35	0.521261	60	-
310-319	30	475.4	50.1	39	485.3	45.97	-0.42434	67	-
320-329	40	522	48.51	56	516	52	0.288356	94	-
330-339	56	564.9	55.04	51	591.5	68.13	-1.11574	105	-
340-349	29	627.8	73.54	37	639.4	73.8	-0.31744	64	-
350-359	14	661.1	45.9	29	698.7	63.85	-1.05271	41	-
360-369	5	678.4	65.11	10	725.9	36.49	-0.85357	13	-
370-379				3	763.3	14.57			

G. ATER: MEAN WEIGHT AT SIZE
T-TEST: MALES VS FEMALES

	MALES			FEMALES				
SIZE CLASS	N	MEAN WT	SD	N	MEAN WT	SD	t-TEST	df	SIG DIF (Y=*/N=-)
200-209	2	175.6	4.65						
210-219	5	182.1	6.91						
220-229	7	196.3	37.4	2	165.5	21.92	0.647578	7	-
230-239	12	239	22.4	7	217	27.52	0.909791	17	-
240-249	47	263.8	24.46	11	4	30.69	1.218058	56	-
250-259	60	292.2	30.56	22	241.3	53.65	0.628912	80	-
260-269	56	322.6	37.54	27	279	34.58	-0.13611	81	-
270-279	32	341.7	44.4	60	324.9	30.85	-1.20203	90	-
280-289	10	366.8	43.3	69	361.5	46.58	-0.95684	77	-
290-299				44	395.9	41.23			
300-309				25	434.2	43.58			
310-319				13	476.4	66.79			
320-329				2	492.6	21.21			

Appendix IIb:

G. FELICEPS: MEAN OBSERVED LENGTH AT AGE
T-TEST: MALES VS FEMALES

	MALE			FEMALE					
AGE	N	MEAN FL	SD	N	MEAN FL	SD	t-TEST	df	SIG DIF (Y=*/N=-)
0	34	63.1	14.861	34	63.1	14.861	0	66	-
1	20	116.9	11.081	20	116.9	11.081	0	38	-
2	36	156	9.549	36	154	8.978	0.457995	70	-
3	21	178.7	7.836	24	177.6	9.781	0.208963	43	-
4	12	208.8	17.309	20	195.4	14.551	1.151833	30	-
5	15	233.3	18.512	16	216.6	13.923	1.432607	29	-
6	22	257.6	15.786	23	243.1	20.277	1.348264	43	-
7	16	285.2	15.182	10	267	15.556	1.468821	24	-
8	19	296.4	13.823	14	294.3	11.211	0.239117	31	-
9	30	311.9	11.657	27	309	11.769	0.466664	55	-
10	32	316.9	12.438	19	320.7	8.233	-0.63472	49	-
11	16	329.7	8.986	17	324.9	16.913	0.532090	31	-
12	14	329.8	8.773	19	324.4	13.045	0.702688	31	-
13	8	336.9	4.051	20	333.3	7.941	0.717615	26	-
14	4	340.4	6.539	9	342.3	10.38	-0.18687	11	-
15	4	349	6.726	9	346.9	6.274	0.268816	11	-
16	9	350.8	6.2	9	351.5	5.804	-0.12370	16	-
17				7	362.9	5.336			
18				1	373				

G. ATER: MEAN OBSERVED LENGTH AT AGE
T-TEST: MALES VS FEMALES

	MALE			FEMALE					
AGE	N	MEAN FL	SD	N	MEAN FL	SD	t-TEST	df	SIG DIF (Y=*/N=-)
0	18	80.3	10.975	18	80.3	10.975	0	34	-
1	7	111.9	6.669	7	111.9	6.669	0	12	-
2	15	140.2	14.727	11	149.3	13.207	-0.82066	24	-
3	15	165	13.846	8	175.1	10.453	-0.94942	21	-
4	15	185.7	16.36	7	196.3	10.563	-0.86013	20	-
5	14	198.9	11.973	14	209.6	12.9	-1.13816	26	-
6	10	219.6	9.153	6	223	10.746	-0.33084	14	-
7	16	241.5	8.189	4	232	10.893	0.890583	18	-
8	19	250	6.123	11	248.9	9.126	0.190398	28	-
9	24	251	8.477	12	252.8	7.146	-0.32587	34	-
10	23	254.9	8.155	12	262.3	7.818	-1.30096	33	-
11	14	257.6	8.723	7	270.3	5.88	-1.87873	19	-
12	10	264	4.566	25	278.1	7.253	-3.18841	33	*
13	5	268	4.301	26	281	8.476	-2.08355	29	*
14	3	272.7	8.083	26	287.2	7.014	-1.57516	27	-
15	6	284.5	4.506	12	295	3.668	-2.56912	16	*

Appendix IIc:

G. FELICEPS & G. ATER: BACK-CALCULATED MEAN FORK LENGTH AT AGE
T-TEST: MALES VS. FEMALES

G. FELICEPS

		MALES MEAN			FEMALES MEAN				SIG DIF
AGE	N	BCLC FL	SD	N	BCLC FL	SD	t-TEST	df	(Y=*/N=-)
0	11	77.5	12.14	16	82.2	9.12	-0.56442	25	-
1	11	113.4	16.28	16	120.3	15.21	-0.55943	25	-
2	11	149.4	19.25	16	152.1	17.18	-0.18922	25	-
3	11	181.5	19.8	16	177.4	17.81	0.278326	25	-
4	11	208.5	16.65	16	200.8	16.64	0.590542	25	-
5	11	230.8	14.93	16	221.5	14.13	0.817074	25	-
6	11	248.1	13.84	16	238.9	13.49	0.859454	25	-
7	11	261.3	15.57	16	255.4	13.48	0.518537	25	-
8	10	275.3	16.22	16	272.2	13.2	0.261392	24	-
9	10	288.8	16.58	15	285	14.21	0.302307	24	-

G. ATER

		MALES MEAN			FEMALES MEAN				SIG DIF
AGE	N	BCLC FL	SD	N	BCLC FL	SD	t-TEST	df	(Y=*/N=-)
0	15	85.3	9.02	10	82.3	9.12	0.405097	23	-
1	15	116	10.45	10	117.7	8.77	-0.21665	23	-
2	15	141.8	12.71	10	148	11.88	-0.61760	23	-
3	15	166.6	14.58	10	171.8	11.79	-0.48302	23	-
4	15	186.9	14.58	10	191	12.58	-0.36976	23	-
5	14	204.6	16.21	10	209	10.51	-0.39771	22	-
6	12	215.7	12.46	9	221.7	8.06	-0.66309	19	-
7	11	226.6	10.86	8	235.7	7.05	-1.09347	17	-
8	11	236.5	10.97	4	247.6	7.9	-1.00746	13	-

APPENDIX III

A) An example of the method used in the normalisation of age-length keys and in the construction of catch-curves using the Ricker[1] method for G. feliceps males:

i) An age-length key is constructed using the sub-sample of aged fish as follows:

SIZE	AGE												ALL
CLASS	4	5	6	7	8	9	10	11	12	13	14	15	16	AGES
200-209	3	1												4
210-219	2	3	1											6
220-229	2	1	0											3
230-239	2	5	2											9
240-249		1	2											3
250-259		3	6	1										10
260-269		1	5	1										7
270-279			5	2	3									10
280-289			1	6	2									9
290-299				3	4	4	3							14
300-309				3	5	6	6							20
310-319					4	7	5	2	2					20
320-329						10	13	3	4					30
330-339						1	5	10	6	6	3			31
340-349								1	2	2	0	2	2	9
350-359											1	2	6	9
360-369													1	1
ALL SIZES	9	15	22	16	18	28	32	16	14	8	4	4	9	195

Appendix III contd.

ii) Through row-wise division, the number of fish of each age in a size-class is divided by the total number of fish in the size-class.

SIZE CLASS	AGE 4	5	6	7	8	9	10	11	12	13	14	15	16	ALL AGES
200-209	0.75	0.25												4
210-219	0.33	0.50	0.16											6
220-229	0.66	0.33	0.00											3
230-239	0.22	0.55	0.22											9
240-249		0.33	0.66											3
250-259		0.30	0.60	0.10										10
260-269		0.14	0.71	0.14										7
270-279			0.50	0.20	0.30									10
280-289			0.11	0.66	0.22									9
290-299				0.21	0.29	0.29	0.21							14
300-309				0.15	0.25	0.30	0.30							20
310-319					0.20	0.35	0.25	0.10	0.10					20
320-329						0.33	0.43	0.10	0.13					30
330-339						0.03	0.16	0.32	0.19	0.19	0.10			31
340-349								0.11	0.22	0.22	0.00	0.22	0.22	9
350-359											0.11	0.22	0.66	9
360-369													1.00	1
ALL SIZES	9	15	22	16	18	28	32	16	14	8	4	4	9	195

Appendix III contd.

iii) Using row-wise multiplication of the table by the total size-frequency sample, followed by column-wise addition, a single value is obtained for each age. This represents the normalised fish number at age. The natural logs of these values are plotted against age in the construction of a catch-curve.

SIZE	AGE													TOTAL
CLASS	4	5	6	7	8	9	10	11	12	13	14	15	16	L-F
200-209	0.00	0.00												0
210-219	0.33	0.50	0.17											1
220-229	0.67	0.33	0.00											1
230-239	0.44	1.11	0.44											2
240-249		2.67	5.33											8
250-259		9.30	18.60	3.10										31
260-269		5.00	25.00	5.00										35
270-279			24.50	9.80	14.70									49
280-289			6.33	38.00	12.66									57
290-299				16.07	21.42	21.42	16.07							75
300-309				10.95	18.25	21.90	21.90							73
310-319					16.00	28.00	20.00	8.00	8.00					80
320-329						42.66	55.46	12.80	17.06					128
330-339						4.35	21.77	43.54	26.12	26.12	13.06			135
340-349								11.22	22.44	22.44	0.00	22.44	22.44	101
350-359											5.33	10.66	32.00	48
360-369													13.00	13
	1.44	18.91	80.37	82.92	83.04	118.3	135.2	75.57	73.64	48.57	18.39	33.11	67.44	
Log_e:	0.37	2.94	4.39	4.42	4.42	4.77	4.91	4.33	4.30	3.88	2.91	3.50	4.21	

Appendix III contd.

IV) Catch-curve constructed using the normalised age-length key. Note the biased values obtained for the older age classes.

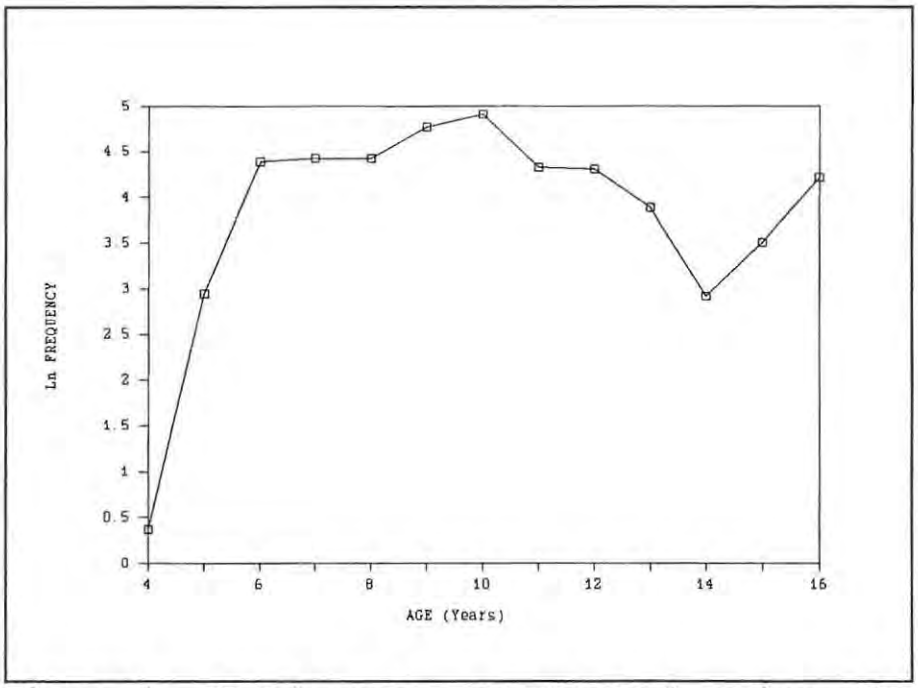

Figure 1: Catch-curve constructed using the Ricker[1] method.

Appendix III contd.

B) An example of the method used in the construction of catch-curves using the Ricker[2] method described for G. feliceps males:

SIZE CLASS Lower Limit	Upper Limit	Mid-Range	N	t1	t	dt	t	LnN/dt	Data range (*) used in catch-curve
210	219	214.5	1	5.26	5.61	0.35	5.43	1.05	*
220	229	224.5	1	5.65	6.02	0.37	5.83	0.99	*
230	239	234.5	2	6.06	6.46	0.394	6.26	1.62	*
240	249	244.5	8	6.50	6.92	0.421	6.71	2.94	*
250	259	254.5	31	6.97	7.43	0.452	7.20	4.23	*
260	269	264.5	35	7.48	7.97	0.488	7.72	4.27	*
270	279	274.5	49	8.02	8.55	0.531	8.28	4.53	*
280	289	284.5	57	8.61	9.2	0.581	8.9	4.59	*
290	299	294.5	75	9.26	9.91	0.642	9.58	4.76	*
300	309	304.5	73	9.98	10.7	0.718	10.33	4.62	*
310	319	314.5	80	10.78	11.6	0.813	11.18	4.59	*
320	329	324.5	128	11.69	12.63	0.938	12.15	4.92	*
330	339	334.5	135	12.74	13.85	1.108	13.27	4.80	*
340	349	344.5	101	13.99	15.34	1.353	14.63	4.31	*
350	359	354.5	48	15.51	17.25	1.739	16.32	3.32	*
360	369	364.5	13	17.47	19.91	2.437	18.58	1.67	-

N = The number of fish in the size frequency distribution sample

t1 = the age of fish at the lower limit of the size class,

t2 = the age of fish at the upper limit of the size class,

dt = the time needed to grow from the lower to the upper limit of a given size class

t = the relative age corresponding to the mid-range of the size class in question.

Appendix III contd.

Since growth is not linear, the larger size classes will contain more age groups than smaller size classes. To compensate for this a correction factor is used in which the numbers of fish in each age class are divided by 'dt'. The natural logs of these corrected ages are then plotted against relative age in the construction of a catch-curve.

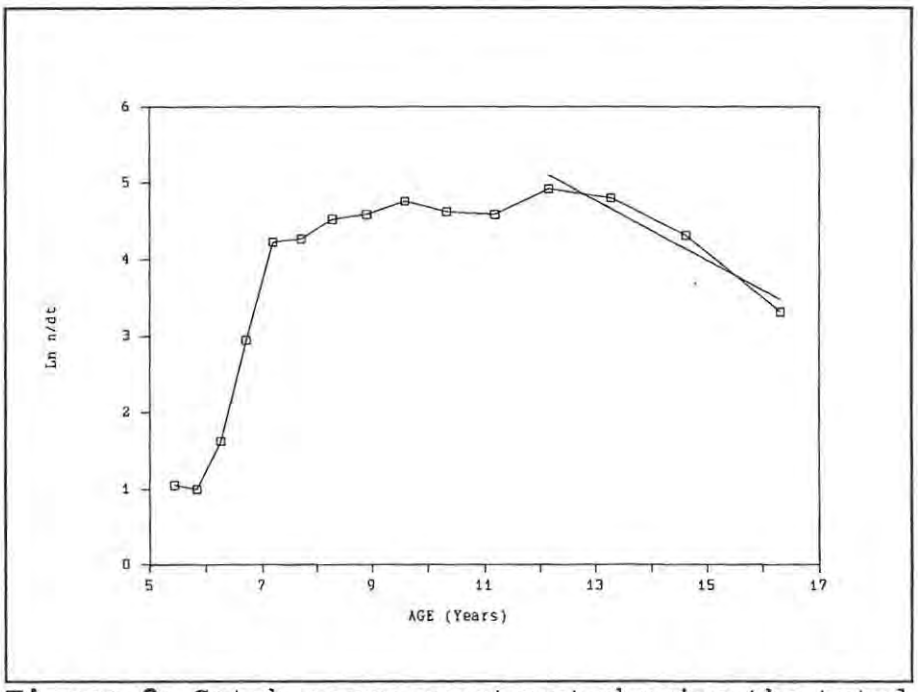

Figure 2: Catch-curve constructed using the total size-frequency distribution.

APPENDIX IV

An example of the Holden & Meadows (1964 in Holden 1977) model as applied to G. feliceps female data.

The model estimates the number of female young born to an initial cohort of 1000 fish. The natural mortality rate was 0.101 and total mortality rate was 0.318 from the age of recruitment onwards (11 years). Age at sexual maturity was attained at approximately 9 years (see Table XXVI). Mean fecundity was 49 and the sex ratio of young was taken as 1:1. Fecundity did not increase as a function of body size. Given the above data the following stock sizes can be determined:

cohort at 9 years = $1000e^{-0.909} = 402.93$

cohort at 10 years = $402.93e^{-0.101} = 364.22$

cohort at 11 years = $364.22e^{-0.318} = 265.01$

The cohort survival and number of female embryos were calculated for values of M 25% above and below the Pauly (1980) estimate. These values of M were also used in the Beverton-Holt yield-per-recruit and spawner biomass-per-recruit models.

Age in years	No. of fish			No. of female embryos		
	M = 0.101	M = 0.078	M = 0.126	M = 0.101	M = 0.708	M = 0.126
9	402.93	495.59	321.74	9871.78	12141.96	7882.63
10	364.22	458.41	283.65	8923.39	11231.05	6949.43
11	265.01	333.54	206.38	6492.75	8171.79	5056.31
12	192.82	242.68	150.17	4724.09	5945.66	3679.17
13	140.30	176.58	109.61	3437.35	4326.21	2685.45
14	102.08	128.48	79.5	2500.96	3147.76	1947.75
15	74.27	93.48	57.84	1819.62	2290.26	1417.08
16	54.04	68.02	42.09	1323.98	1666.49	1031.21
17	39.32	49.50	30.62	963.34	1212.75	750.19
18	28.61	36.01	22.28	700.95	882.25	558.60
Total number of female embryos				40758.21	51016.18	31957.82