A CONTRIBUTION TOWARDS THE TAXONOMY OF THE ICHTHYOPLANKTON SPECIES COMMUNITY AND AN UNDERSTANDING OF ITS DYNAMICS ALONG THE SOUTH-EAST COAST OF SOUTH AFRICA.

A thesis submitted in fulfilment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

of

RHODES UNIVERSITY

by

AIDAN DAVID WOOD

October 1998

ABSTRACT

This study was prompted by the need to remedy the situation that existed with respect to the poor status of our knowledge regarding the ichthyoplankton assemblage of the nearshore region along the south-east Cape coast of South Africa. The first chapter provides a brief introduction to the field of ichthyoplankton research and includes a summary of the status of research in southern Africa and an explanation of early life history terminology. The selection of all sample sites, times and strategies is also outlined.

The study area along the south-east Cape coast with respect to its location, climate and physical oceanography is described in the second chapter, as is the gear used, bongo nets and an RMT1x6. A sampling protocol for the use of bongos from a small ski-boat, and the RMT from the research vessels, and for the handling and processing of samples was established. The selection of Middlebank as the main monthly sampling site within the Tsitsikamma National Park (TNP) was based on taxonomic diversity as well as logistical and safety constraints.

The effect of mesh size and time of sampling with bongo nets on the catchability of ichthyoplankton was investigated in chapter three. Most data was accumulated during Sea Fisheries research cruises, with additional collections coming from the National Parks vessel. Although the differences were not significant, the 505 μ mesh nets captured larger larvae, with catches comprising higher percentages of flexion and postflexion larvae. Larval concentration and size were consistently greater in samples from periods of reduced light intensity, but significant differences were the exception. It was decided that sampling with 505 μ mesh nets during daylight would provide a representative sample of the available ichthyoplankton assemblage, while at the same time being the most practical and least time consuming with respect to handling, clogging and backflushing.

In chapter four, the early life history stages of thirty of the seventy-five taxa sampled are described, reflecting the paucity of information which existed on the ichthyoplankton of the nearshore zone in the south-east Cape. These descriptions are seen as an important contribution towards any future research efforts in the region, but as many of these descriptions are based on few or single specimens, it is realised that the description of egg and larval stages will be an ongoing process.

Based upon the data collected during this study, an ichthyoplankton species checklist was established in chapter five. Seventy-five taxa of fish larvae were identified to either family, genus or

species level. A number of squid para-larvae were also encountered. Similarities and discrepancies with a previous survey in the region are presented. The temporal distribution of eggs and larvae between August 1993 and October 1996 was established. and the spatial distribution of ichthyoplankton along an offshore transect was determined between January 1995 and May 1996. Only 7 species from Middlebank and twelve from all stations combined displayed seasonal trends. with most of these being prevalent during winter months. Egg production. both over Middlebank and from all stations combined, appeared to be consistent. with no seasonal trends. Based upon the results from the offshore transect samples. it would appear that a single ichthyoplankton assemblage exists from Storms River out to fifteen nautical miles. Although a variety of statistical methods were applied to the data during this study. low egg and larval concentrations and a low sampling frequency meant that results had to be interpreted carefully.

Chapter six describes the preliminary investigation into the vertical distribution of eggs and larvae. During two research cruises. discrete depth sampling using an RMT1x6 net was performed. with the majority of samples being accompanied by physical data provided by a CTD rosette sampler. No definite patterns could be seen as larval concentrations were low. and the short time scale did not allow for the identification of any diel migratory patterns. The relationship between total larvae and the physical environment was poor. The only possible relationship was that between plankton volume and total egg and total larval concentrations.

The TNP may play an important role in the conservation of reef fish and the seeding of nearby fishing grounds through the export of pelagic eggs and larvae. Chapter seven describes a preliminary investigation into the dispersal potential of ichthyoplankton from the TNP. Based upon longshore currents determined from drogues. ADCP vectors and current meter readings. it was clear that if larvae were passive drifters. the potential for their dispersal from the TNP did exist. This pilot study showed that future work should concentrate not only on the oceanographic aspects. but on behavioural aspects of larvae which may enhance or retard dispersal.

In the final discussion. it is emphasised that while this study went a long way to increasing our knowledge of the nearshore ichthyoplankton community. the true picture of the temporal and spatial dynamics of the species assemblage may only be revealed once more intensive sampling has been performed. The resolution of the early life history stages of the sparids and the identification of eggs to species level are seen as priorities for the near future. A complete species checklist for the TNP is provided based upon previous surveys (both on adult and larval fishes). this work and personal observations. A total of 171 species of fish from 70 families were identified. illustrating

that the eggs and larvae of many species in the TNP have yet to be sampled. A brief description of the collaborative effort which is envisaged for the TNP over the next few years is provided.

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ACKNOWLEDGEMENTS

My first words of thanks are extended to Colin Buxton who provided the support and impetus for this project during its early stages, and to Rob Tilney for his invaluable experience and expertise on the small picture in Tsitsikamma. To Jeff Leis who had to listen to the ramblings of an ichthyoplankton amateur when I met him at the Australian Museum in 1994 and then who graciously gave me the tour of their collection, thank-you. During the latter stages of the work, Colin Buxton, Warwick Sauer and Lisl Griffioen-Paterson all helped with the final arrangement of this manuscript and are thanked for their input and comments.

This project would not have been possible were it not for the generosity of South African National Parks, and in particular the staff of the Tsitsikamma National Park. The past and present park wardens, Dennis Bouwer and Corrie Pieterse respectively, are acknowledged for their facilitation, support, enthusiasm and interest in the project. A special thanks must be extended to John Allen, skipper of *Natpark Aonyx*, for all his time and advice, as well as the many anecdotes which helped pass the many hours spent at sea. He has yet to meet his match when it comes to handling that boat in any kind of sea. The crew of *Aonyx*, Karools Pieterse and Johnson Ndawo, were invaluable when it came to launching and recovering the boat, manhandling nets and drogues and helping with any eventuality without hesitation - even when it meant going for a swim in the mooring gully while fully clothed - twice.

The captains, crew and scientists of the R.S. *Algoa* during voyages number 6 and 15, and the R. S. *Africana* during voyages number 131 and 135 are thanked for their help, hospitality and humour. Thanks too for their patience and understanding during the late night samples and for pretending not to notice when I turned a shade of green during heavy weather. ADCP data during the *Africana* cruises was made available by Heather Sessions, Christine Illert and Alan Boyd, while Heather and Christine also performed the CTD dips when required - thanks.

Additional help always seemed to be at hand when it came to sampling, both from *Aonyx* and the Sea Fisheries research ships. The following people are thanked for pulling nets, launching and recovering drogues, scribing data, storing samples and other miscellaneous tasks during field trips: Rob Tilney, Colin Buxton, Amanda M^{c}Phail, John Allen, Karools Pieterse, Johnson Ndawo, Jerome Davis, Steve Brouwer, Eckart Schumann, John Churchill, Colin Attwood and Piet Claasen. The assistance of Alan Rees, Mark Bantich, Amanda M^{c}Phail and Anthony Booth in sorting samples in

the lab during the early stages of this project was greatly appreciated. Jeff Leis, Lynnath Beckley, Helen Larson, and Rob Tilney are thanked for their help in identifying some of the larvae. A big thanks to Elaine Heemstra for her time and patience in educating me in the delicate art of larval illustration, and to Joan Wright for her help with staining and clearing of specimens.

Thank-you to Sarah Radloff from Maths and Stats at Rhodes University for her guidance and advice on matters statistical and to Debbie Brody at the Cartography unit at Rhodes for the maps, cluster diagram, ADCP illustrations and wind/current figures.

The following organisations are thanked for their financial backing at various stages during the course of the project. Rhodes University, Foundation for Research and Development, Sea Fisheries Fund, National Parks Board, Nestlé, and First National Bank. In addition South African National Parks are thanked for sponsoring boat fuel and providing accommodation during field trips.

I will never forget the unique hospitality offered by John, Jean, Jessica and Jeremy Allen. Their home was always open and they made sure we were never left wanting for anything - thanks for everything. A final heartfelt thanks to my parents, Aidan and Norma, for their patience, love and understanding, and to Angus and Lisl for their support during a particularly difficult time and for showing me what true friendship is all about.

CHAPTER 1 - GENERAL INTRODUCTION, SITE SELECTION AND SAMPLING PROTOCOL

In order to fully understand the ecological role filled by fishes, all aspects of their life history, including the complexities of the egg and larval stages, should enjoy equal scrutiny. It is well known that in most cases teleost eggs and larvae exist in a world that, apart from the medium of water, is vastly different from the one which supports the other life history phases. Morphologically, physiologically and behaviourally, marine ichthyoplankton differ so incredibly that they are at times considered different eco-species to adult and sub-adult fish (Leis & Rennis 1983). Regardless of adult habits, distribution or systematic affinities, the majority of marine fish are generalists (*sensu* Balon 1975, 1981), spawning pelagic eggs (Houde 1987) which after external fertilisation float freely amongst the plankton (Omori & Ikeda 1984a) at the mercy of the ocean's biotic and abiotic environment. Although referring to coral reef and tropical fishes, the reasons proposed for this phenomenon of pelagic early stages can be expanded to include the fishes along southern Africa's temperate coastline. Barlow (1981) suggested that the primary reason is to ensure the long distance dispersal of the planktonic propagules, while Johannes (1978) voiced his opinion that eggs and larvae in open water were less prone to predation, assuming that this outweighs the potential for mortality as a result of advection (Boehlert, Watson & Sun 1992). It has been further postulated that losses due to advection are reduced by adult fish spawning when currents and winds are weakest and mesoscale eddies ensure retention in the vicinity of gamete release (Johannes *op. cit.*; Lobel & Robinson 1986; Lobel 1989) as was demonstrated by Boehlert *et al.* (*op. cit.*) for locally spawned eggs and larvae from Johnston Atoll in the central Pacific Ocean.

Egg characteristics are species specific as are developmental times which are mediated to a large extent by temperature (Kendall, Ahlstrom & Moser 1984). The yolk-sac larvae which emerge from the eggs are poorly developed, feeble swimmers, and still very much unable to fend for themselves. Nourishment comes from the remnant yolk-sac until their internal life support systems are functional and they can begin feeding on plankton. At this stage, certain larval characters begin to emerge which are considered to be adapted specifically for this period of the life cycle. This in part prompted Moser (1981) to declare that marine fish larvae exist in their own evolutionary domain which is unique from that of adults and that they have

been provided with the necessary specialisation's in order to ensure maximum survival in a particularly harsh and demanding environment. The gradual emergence of adult characters signals the last phase of larval development prior to metamorphosis into juveniles. This transformation may be prolonged or abrupt, and although some will continue to exist as pelagic juveniles and adults, to the majority metamorphosis is a change in appearance and a change in habitat from pelagic to demersal (Kendall *et al.* 1984). The duration of the planktonic phase and the numerous larval stages tends to be species specific but may vary intra-specifically, depending on geographic location, temperature, light, food availability and food quality (Houde *op. cit.*).

As is always the case in nature there are exceptions to the general rule. Adults of certain species do not spawn pelagic eggs but instead exhibit increased parental investment (Gross & Sargent 1985) by laying fewer but larger demersal eggs which may be adhesive and guarded, producing well developed larvae with advanced larval characteristics (Marshall 1953). Many of the deep-sea fishes and coastal marine species develop from demersal eggs which may be guarded by the parents who have built a protective structure such as a nest, e.g. blennies (Dotsu & Moriuchi 1980; Almada & Serraosantos 1995), gobiesocids (Ruck 1973), gobiids (Leis & Rennis 1983; Lindström & Wennström 1994), the *Amphiprion* and *Premnas* species of pomacentrids (Fautin & Allen 1992) and the endemic sparid *Spondyliosoma emarginatum* (Van Bruggen 1965; Penrith 1972; Buxton & Garratt 1990). In the seacatfishes (Ariidae) eggs and yolk-sac larvae are carried around in the mouth of the male parent (Mansueti & Hardy 1967) until absorption is complete. At this stage the majority of adult features are visible and when larvae are finally released they are mostly demersal but sometimes hang at the surface. Perhaps the most extreme form of parental investment is seen in viviparous species such as some of the zoarcids, poeciliids, embiotocids and clinids (Wourms 1981; Smith 1986d; Prochazka & Griffiths 1992) where embryos are nourished from maternal structures. The alternative reproductive guilds in fishes which include the guarders, mouth brooders and bearers can be regarded as specialised when compared to non-guarders or pelagic spawners (Balon 1975, 1981; Bruton 1989). These specialised forms generally have low fecundity, large eggs with a large yolk, and invest a large amount of energy in fewer young. The precocial young which characterise these specialists are well developed and cope best in a stable, crowded environment where they are subject to density-dependent mortality (Balon 1978,

1983). In some cases the embryo period is long and the larval phase is bypassed altogether with direct development into a juvenile. The advantages of increased parental investment in the forms described above appears to be reduced predation and dispersal. The production of many incompletely developed young by generalist broadcast spawners is, however, equally effective in ensuring survival under a different set of circumstances where the environment is uncrowded, unstable and characterised by density-dependent mortality (Balon 1981, 1983; Bruton 1986).

The History of Ichthyoplankton Research in Southern Africa

The waters around the Cape of Good Hope were the site for the first ichthyoplankton samples in southern Africa just after the turn of the century. The Colonial Government of the time, eventually succumbing to the protests of line fishermen that trawling and netting was affecting stocks because the practice destroyed eggs and spawn lying on the bottom, commissioned an investigation into these early life history stages. Using fine mesh nets and eggs from mature fish procured aboard the Government steamer, Gilchrist (1903, 1904) made the first contributions to ontogeny and taxonomy of ichthyoplankton, describing various stages of development of 41 species. Five publications later (Gilchrist 1914, 1916, 1918, 1921; Gilchrist & Hunter 1919), and with new material from Table Bay, the total number of described species was 68. With the passing of John Gilchrist in 1926 ichthyoplankton studies were shelved for almost three decades until Davies (1954) emerged with what was to be the first of many studies of the commercially important pilchard, *Sardinops sagax*. The early fifties produced two more works, both on other commercial species. Matthews & De Jager (1951) provided a description of the early stages of the shallow water hake *Merluccius capensis*, while De Jager (1955) described the ontogeny of the snoek *Thyrsites atun* from artificially fertilised eggs up to 9 day old larvae. Although plankton nets were being used during research voyages between 1950 - 1967 (see Haigh 1972a), the only trace of ichthyoplankton work during that period was the description of egg and larval stages of the southern conger eel *Gnatophis capensis* by Castle (1968, 1969). The next efforts emerged in the 1970s, and were to mark the resurgence of ichthyoplankton work in this country. The emphasis was clearly still on teleost species which fulfilled an important function in the West Coast commercial fishery, such as *M. capensis*, *T. atun*, the jacopever *Helicolenus dactylopterus* (Haigh *op. cit.*), maasbanker *Trachurus trachurus capensis* (Haigh 1972b; King, O'Toole & Robertson 1977), *S. sagax* (Louw & O'Toole 1977), and the anchovy *Engraulis japonicus* (King, Robertson & Shelton 1978). The Cape Egg and Larval Survey (CELP) which comprised 13 research cruises

in 1977/78 was aimed at sampling the ichthyoplankton of the Benguela region from Stil Bay in the east to just north of the Olifants River on the west coast. Once again the focus of attention was on pelagic species of commercial importance (e.g. Dudley, Field & Shelton 1985).

It was inevitable that ichthyoplankton work on commercial teleost species would make inroads to Namibian waters, and this came about in the late 1970s with the first published work being that of Ahlstrom, Moser & O'Toole (1976) on the onderbaadjie *Lampanyctodes hectoris*. Similar to the trend being followed in South Africa, workers in Namibian waters concentrated their efforts on commercial trawl species such as *S. sagax* (King 1977a, b), *E. japonicus* (King 1977a), *T. capensis*, *M. capensis*, the west coast sole *Austroglossus microlepis* (O'Toole 1977a, b, 1978a) and East coast roundherring *Etrumeus teres* (O'Toole & King 1974) during the South West African Pelagic Egg and Larval Survey (SWAPELS) program. In addition, O'Toole (1978b) performed an in depth study on the pelagic goby *Sufflogobius bibarbatus* from the same region. Based on material collected between October 1978 and April 1979, Boyd & Badenhorst (1981) estimated an early growth rate of 0.6 mm/day at 15°C for the first two weeks in *S. sagax* sampled off Namibia. A recent review by Olivar & Shelton (1993) deals with the distribution of the Benguela ichthyoplankton assemblage with respect to season, depth and oceanographic features, based on data collected from oblique bongo hauls and discrete depth Rectangular Midwater Trawl (RMT) tows during research voyages between August 1977 and April 1986.

Due to the concentration of research on commercial species along the West Coast, aspects of ichthyoplankton dynamics were virtually ignored along the eastern seaboard of South Africa, although research into eggs and larvae from east coast estuaries enjoyed some attention (see below). Not surprisingly, the first publications to emerge from the eastern seaboard region were also concerned with the commercial pelagic species *S. sagax*, *E. japonicus* and the Redeye roundherring *Etrumeus whiteheadi*. Even though research voyages included plankton sampling since 1951, the first evidence of pilchard eggs being caught was in 1960. During R.V. *Meiring Naude* voyages in 1973 between Algoa Bay and Ponta Do Oura the highest densities of *S. sagax* eggs were found towards the end of winter and in mid-summer between Algoa Bay and the Bashee River, with anchovy eggs also peaking in December in the same area (Anders 1975). Using drift cards to map current patterns along the south-east coast, Shelton & Kriel (1980) surmised about

larval mortality in all three species in relation to westward or eastward dispersal into areas comprising two very different water regimes.

Apart from the many field studies originating in the early seventies, this period also marked the beginning of the experimental stage with work being performed in the laboratory to assess the effects of various physical parameters on egg incubation times and development rates (King 1977b, King *et al.* 1977; King *et al.* 1978). This was taken further by Brownell (1979) who investigated the water quality requirements for first feeding in teleost larvae. In this study he presented descriptions (some augmenting original descriptions by Gilchrist) and illustrations for 40 species common to the inshore plankton of the Cape of Good Hope. He further described the development of *E. japonicus* and *S. sagax* from laboratory reared animals (Brownell 1983). More recent works revolved around the artificial spawning and rearing of two species which are important in the inshore linefishery, namely carpenter *Argyrozona argyrozona* (Davis & Buxton 1996) and Roman *Chrysoblephus laticeps* (Davis 1996).

The first appearance of combining ichthyoplankton distributional studies with physical oceanography had the distinction of being performed in Namibian waters when O'Toole (1977b) related depth distributional patterns of *T. t. capensis* larvae to hydrological factors. This was followed by Badenhorst & Boyd (1980) who similarly looked at larvae and juveniles of *E. japonicus* in the context of hydrological patterns off Namibia. In South African waters, the drift card study mentioned earlier illustrated the westward and eastward movement of water along the south-east coast. Based on their findings, Shelton & Kriel (1980) surmised how this would affect survivability rates of eggs and larvae which would be transported to either nutrient rich cold, upwelled waters on the west coast or warmer, nutrient poor waters on the east coast. Eggs of *S. sagax* in Namibian waters were correlated on both a temporal and spatial scale with plankton and seasonal occurrence, and physical parameters such as temperature and salinity (Le Clus & Kruger 1982; Le Clus 1987). More recent studies were expanded to include East Coast oceanography (e.g. Beckley & Van Ballegooyen 1992). Studies on the interaction between larvae and water body parameters were not exclusive to the oceanic environment and Melville-Smith, Baird & Wooldridge (1981) assessed the extent to which tidal currents were utilised by *Gilchristella aestuaria* in the Sundays Estuary. By maintaining a position close to the bottom *G. aestuaria*

larvae avoided being flushed out to sea during the falling tide and managed a net movement upstream with the initial surge of fast moving water at the start of the flooding tide.

According to the literature, the first studies on teleost eggs and larvae from southern African estuarine systems are attributed to works carried out in the Swartkops Estuary (Melville-Smith 1978; Melville-Smith & Baird 1980), Kromme Estuary (Melville-Smith 1981) and the Sundays Estuary (Melville-Smith *et al.* 1981). In light of the fact that estuaries are perceived as being ideal nursery areas while at the same time supporting recreational and artisanal fisheries many more studies on ichthyoplankton followed. These included taxonomic works (Neira, Beckley & Whitfield 1988; Haigh & Whitfield 1993), tidal effects on egg and larval interchange between the estuarine and surf zone (Beckley 1985; Whitfield 1989a), and studies on species composition, seasonality and abundance (Harrison & Whitfield 1990; Whitfield 1989b, 1994). The ichthyoplankton in estuaries and certain coastal systems further north along the East Coast, including St. Lucia, Kosi and Durban Harbour, have recently been covered in KwaZulu-Natal by Harris & Cyrus (1995a, 1997), Harris, Cyrus & Forbes (1995) and Harris (1996). Extreme meteorological events had prompted an earlier study on the St. Lucia Estuary (Martin, Cyrus & Forbes 1992) to assess the effects of flushing due to cyclone induced floods on the ichthyoplankton assemblage. The specific issue of nursery areas was addressed by Whitfield (1989c) who determined that the surf zone adjacent to the Swartvlei Estuary was acting as a refuge before postlarval juveniles entered the estuary.

Since the mid-1980s oceanic ichthyoplankton research has been largely dominated by two workers who are responsible for over 30 publications between them, either individual attempts, or co-authored with each other or fellow workers. The topics and taxa dealt with by Maria-Pilar Olivar and Lynnath Beckley are numerous and only a few selected papers are quoted here. Many of their papers dealt with taxonomic descriptions and distributional patterns of the early stages of a variety of species, including *Parablennius pilicornis*, *Paracallionymus costatus*, *Diaphus hudsoni*, *Lecanogaster chrysea* and *Lesueurigobius sanzoi* (Olivar 1986, 1987b, c, d, 1989); *Spondyliosoma emarginatum* (Beckley 1989); *Gonorhynchus gonorhynchus* (Olivar & John 1987); *T. t. capensis* and *Symbolophorus boops* (Olivar & Rubiés 1983, 1986); *Merluccius capensis* (Olivar, Rubiés & Salat 1988); *Genypterus capensis* (Olivar & Sabatés 1989); and *Diaphus dilidematus*, *D. brachycephalus*, *D. richardsoni* and *D. mollis* (Olivar & Beckley 1995).

Papers dealing with a host of species or species assemblages and distribution included works from Namibia and both the East and West Coast of South Africa (Olivar 1987a, 1988b, c; Beckley 1986; Beckley & Hewitson 1994; Olivar & Beckley 1994a). The occurrence and potential for dispersal of certain linefish larvae by the Agulhas Current was presented by Beckley (1993) at the 2nd South African Marine Linefish Symposium. Oceanographic or hydrographic features were also discussed with respect to adult spawning strategies, larval distribution and spatial patterns (Sabatés & Olivar 1989; Olivar 1990; Olivar & Beckley 1994b) and the vertical distribution of larvae on the East (Beckley 1994) and West/Namibian coasts (Olivar & Rubiés 1987) also received attention. A comprehensive study by Olivar & Fortuño (1991) in which they gathered all available descriptive and developmental data for teleost eggs and larvae from the Southeast Atlantic region has gone a long way in helping workers identify plankton samples. It is a reference which is quoted in most papers as being an integral part of ichthyoplankton taxonomy in southern Africa, and was used extensively in this study.

Apart from the few studies by Beckley (1985, 1986, 1993), Whitfield (1989c), Tilney & Buxton (1994), Harris *et al.* (1995), Harris (1996), Harris & Cyrus (1996), and Tilney, Nelson, Radloff & Buxton (1996) there is a paucity of work in the nearshore regions where eggs and larvae of fish which are of importance to both trawl and line fisheries are found. The inshore region of South Africa, incorporating the neritic surf zone and nearshore shallow sub-tidal zone along the eastern seaboard, is a difficult habitat to sample efficiently. The ichthyoplankton assemblages found inshore along the coast need to be studied and documented with the aim of filling the void which surrounds this aspect of early life history studies in South Africa. Part of a current project being undertaken at the East Kleinemonde Estuary in the Eastern Cape (Cowley 1998) involves the surf zone ichthyoplankton assemblage and its relation to recruitment of estuarine dependent species. Together with this study, the paucity of information on inshore ichthyoplankton taxonomy, communities and their distribution in the south-east Cape will be addressed.

The Tsitsikamma National Park

The Tsitsikamma National Park (TNP), proclaimed on the 4th December 1964, extends from Oubosstrand (34° 03' 65" S, 24° 11' 65" E) in the east to "Die Punt" (33° 59' 00" S, 23° 34' 06" E)

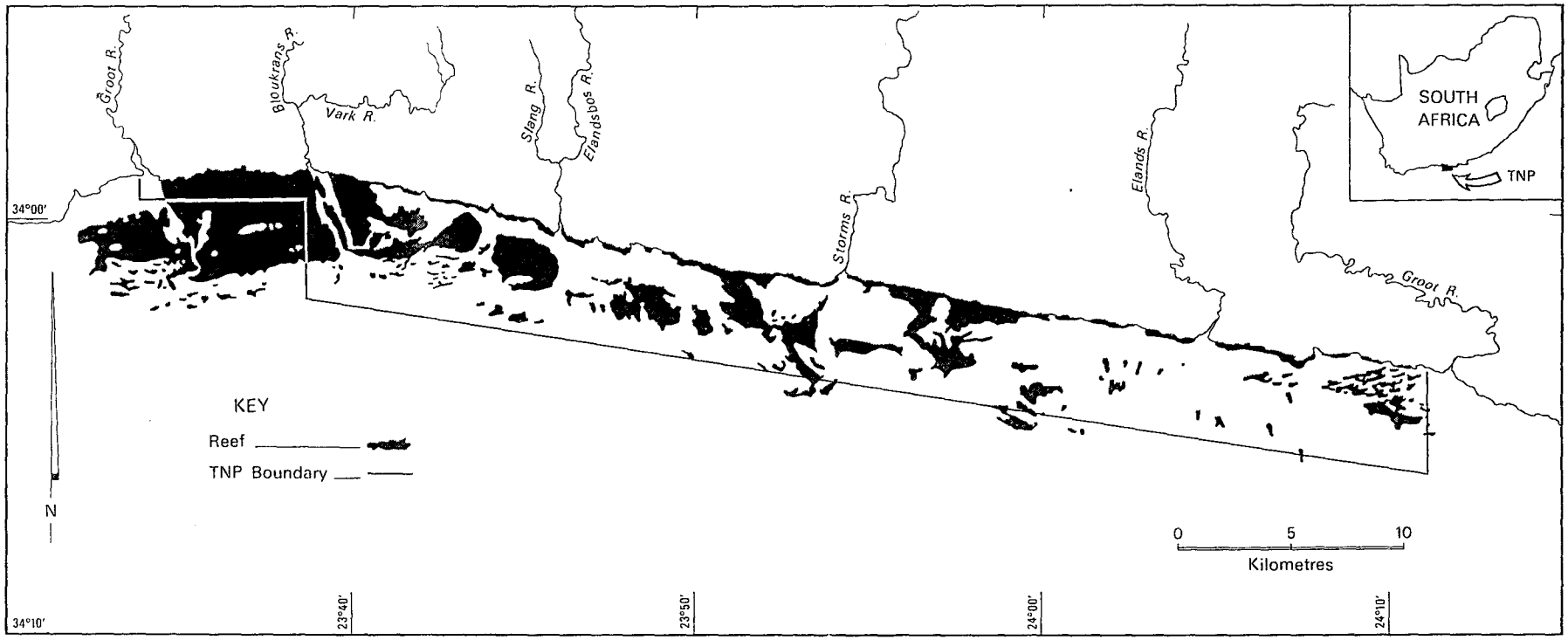
just adjacent to Grootrivier at Nature's Valley in the west (Figure 1.1). This area incorporates 65.75 kilometres of extremely rugged and inaccessible coastline and 36 845 hectares of sea surface area (Hockey & Buxton 1989; Robinson & De Graaf 1994). The seaward border extends from as little as 0.8 km at its western-most end to as much as 5.6 km from the spring low water mark thus incorporating most of the inshore subtidal reef areas. The chief objectives of the park as stated by Robinson & De Graaf (*op. cit.*) are to provide an educational and recreational service for tourists while at the same time acting as a site for further research into both land and sea based ecosystems. In addition, and perhaps most importantly, the marine environment provides a refuge for exploited invertebrate and fish species.

Objectives

The overall objective of the research program conducted by Rhodes University in the TNP along the south-east coast of South Africa, is to determine the importance of large Marine Protected Areas (MPA's) in the conservation of coastal fishes. Work on adult and sub-adult fishes has been ongoing since 1980 and much progress has been made towards achieving this objective. However, work on the early life history stages has, until recently, been neglected. It is the ultimate aim of the ichthyoplankton programme to assess the degree to which eggs and larvae of key linefish species are dispersed from the reserve. It was envisaged that this study would provide the necessary groundwork so that future work efforts could concentrate on achieving this goal. The main objective of this work was to contribute to the knowledge of ichthyoplankton in the nearshore region along the south-east coast of South Africa and to provide information which would lead to a more complete understanding of the life history of the east coast fish species assemblage. This was achieved by dealing with the following aspects:

1. Developing an efficient method of sampling with bongo nets on board a small 21-foot ski-boat, *Natpark Aonyx*, in the coastal zone to ensure that frequent and representative samples could be taken. The effect of mesh size and time of day on the catching efficiency of the gear was also assessed.

Figure 1.1 - The Tsitsikamma National Park situated along the south-east coast of South Africa. The seaward boundary of the Tsitsikamma National Park is displayed and areas of reef are indicated as dark patches. The sample sites at Middlebank (M), Steilkop (S) and Rheeders (R) are indicated.



2. Adding to the present species check-list for the region through the identification of pelagic larvae. Coupled with this is the description and illustration of the early life history stages of those species which have not yet appeared in the literature.

3. Comparing spatial and temporal larval distributional patterns to the known distributions and spawning seasons of adults.

4. Determining the horizontal distribution of eggs and larvae along an offshore transect to assess the degree of retention of inshore, reef associated species.

5. Taking a preliminary look at the extent to which vertical distributional patterns differ over short periods of time and over the diurnal cycle. This aspect was also discussed in the light of certain physical and biological parameters.

6. Performing a preliminary assessment on the dispersal potential of eggs and larvae from within the TNP using historical data and short term, non-continuous oceanographic data obtained by various methods during the course of the study.

7. Finally, recommendations based on these findings, primarily regarding the future expansion of efforts in nearshore ichthyoplankton research, are made. A proposal is presented which is ultimately aimed at answering the question of whether the TNP, and MPA's in general, are acting as ichthyoplankton sinks, or as vital sources for recruitment to adjacent exploited areas.

Site Selection and Sampling Protocol

1. In order to determine an optimum site for obtaining monthly samples, a series of collections were performed as part of the field trials. Financial constraints meant that a site close to the launch site at Storms River had to be chosen. Preliminary surveys (Tilney & Buxton 1994) had shown that distribution for most larval species was homogeneous with no evidence of retention over reef or sand, while eggs were shown to be more concentrated over sandy substrates. It was decided to test three areas located various distances offshore which had differing proportions of reef and sandy substrates as well as different depth profiles.

Factors such as egg and larval abundance, richness at the family level and suitability of the site to the method of sampling which would be used were evaluated. Identification to the family level was used partly because it would facilitate the identification and analysis process and because the findings in Tilney & Buxton (*op. cit.*) were based at this taxonomic level. These tows were also used to determine the homogeneity between samples from the left and right nets and between replicate samples from each site.

Site 1 was Middlebank (Figure 1.1) which is situated approximately 1.4 nautical miles (nm) offshore. It comprises extensive reef with a main pinnacle which rises to 23 metres and drops off rapidly to 40-50 metres before it begins to level out onto sand at 60 metres. Steilkop was the second site (Figure 1.1), situated only 0.25 nm offshore with a maximum recorded depth of only 35 metres. High profile ridges run parallel to the shore line, but the reef area is considerably smaller than at Middlebank and a lot of the area sampled at Steilkop was over sand. The third site was Rheeders (Figure 1.1), a reef complex located 0.5 nm from the shore. It too has high profile ridges running parallel to the coast with blinders that reach to just below the surface at low tide and a few pinnacles which rise to between 10 and 12 metres from the surface. Once again there are patches of sand, but the area covered by the tows was largely over reef. Maximum recorded depth at Rheeders was 48 metres.

2. A brief study of the effect of mesh size on ichthyoplankton catch composition was made possible when three oblique bongo tows were performed on 24 November 1993 within the boundaries of the TNP (Figure 1.2) during voyage #6 on the Fisheries Research Ship *Algoa*. These samples were forwarded by the Sea Fisheries Research Institute (SFRI) for further analysis. The tows were performed between 16h40 and 17h50, with the maximum depth and duration of each tow varying according to the ship's sounding (in parentheses) as follows. 32 m for 2 min 25s (38 m), 44 m for 6 min 55 s (55 m), and 72 m for 5 min 31 s (80 m).

3. Samples for comparing ichthyoplankton catches at different times of the day were taken on five separate occasions using double oblique bongo tows.

28/03/94 - Three replicate tows were performed from *Natpark Aonyx* at four time intervals, namely sunrise (05h55 - 06h38), midday (11h43 - 12h47), sunset (18h13 - 19h18), and late night (21h12 - 22h00). All were performed on Middlebank (Figure 1.2).

29/08/94 - Three tows were performed between 14h40 and 15h25 (light) and a further three between 20h03 and 20h51 (dark) on Middlebank (Figure 1.2) from *Natpark Aonyx*.

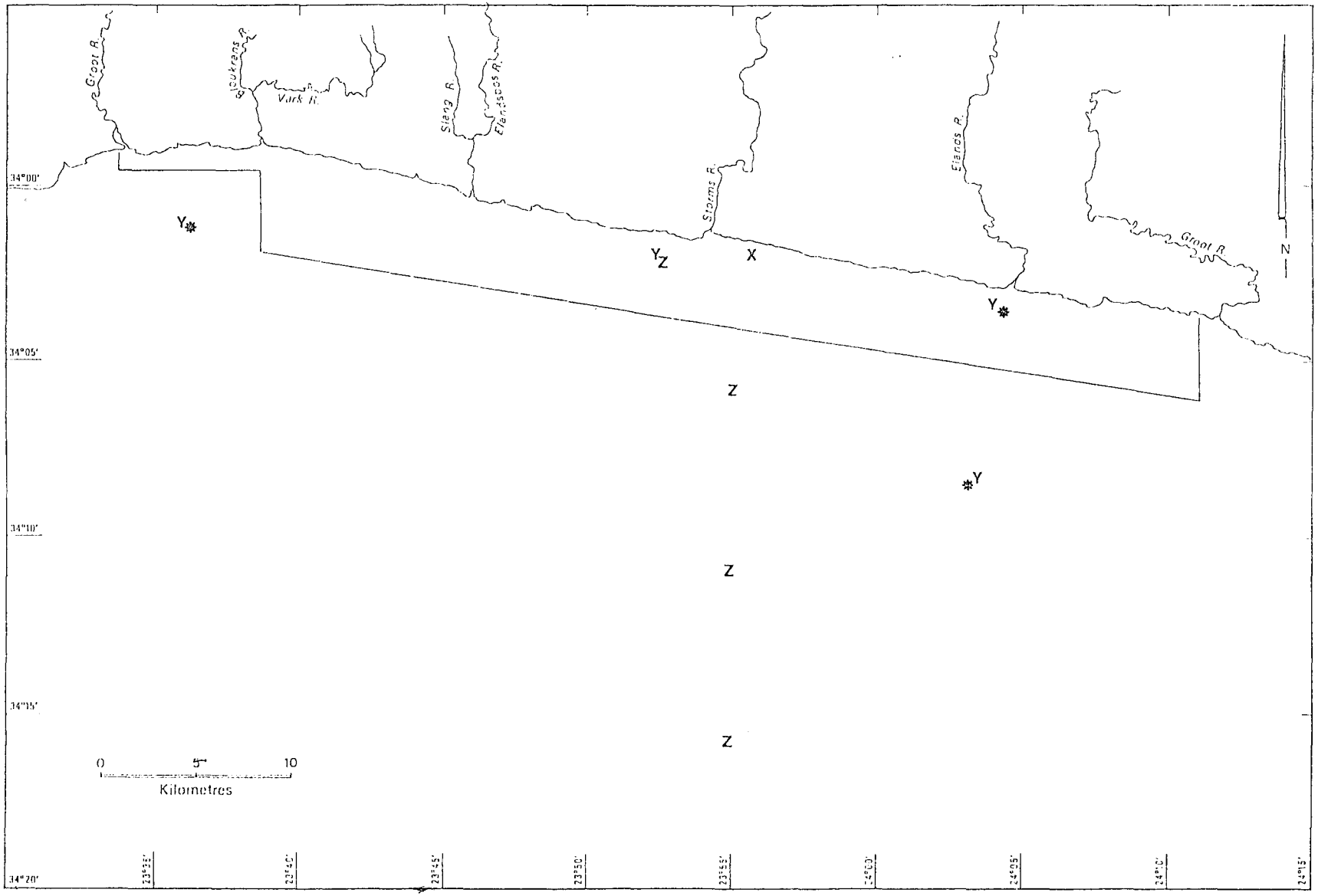
03/11/94 - During the South Coast biomass survey on board the R.S. *Algoa* (voyage #15), three replicate samples were taken at each of three time frames off Elands River in the eastern section of the reserve (Figure 1.2). Sunrise samples were between 04h27 and 05h00, midday collections from 12h53 to 13h43, and sunset samples from 18h01 to 18h48. Depth of oblique tows ranged between 30.9 and 55.8 metres depending on the maximum depth recorded from the ship's sounding.

07-08/10/95 - At mid-afternoon and late night on two consecutive days during voyage #131 on board the R.S. *Africana*, a pair of replicate tows were taken off Elands River mouth (Figure 1.2). Afternoon samples were collected between 16h30 and 17h05 on day 1 and 17h30 and 18h00 on day 2. Late night samples were taken between 22h28 and 23h00 on the first day and 00h00 and 00h32 on the second day.

25-26/04/96 - On two consecutive days during voyage #135 of the R.S. *Africana* tows were carried out near the Bloukrans River mouth (Figure 1.2). On the first day two replicates each were collected at sunrise (06h45 - 07h10), midday (12h15 - 12h46), sunset (17h20 - 17h48) and midnight (11h28 - 11h57). Due to trawling commitments there were no midday samples the following day but replicate pairs were collected between 06h32 and 06h55 at sunrise, 17h30 and 18h02 at sunset, and 22h35 and 23h05 at night.

4. In order to determine the seasonality of ichthyoplankton in the Tsitsikamma region, samples were collected regularly during the period August 1993 to October 1996. Sampling was not possible for certain months due to a host of logistical and meteorological factors and commitments to laboratory work. Unsampled months were September, October and December for 1993; January, April, June, July and October for 1994; May, September and December for 1995; and June, August and September for 1996. Using the seasonal pattern of months from Harris & Cyrus (1995a) a total of seven autumn months and six each for summer, spring and winter were sampled. With the exception of some of the tows in October 1995 and April 1996, which were RMT's from the R.S. *Africana*, all samples were obtained from double oblique

Figure 1.2 - The study area along the south-east coast with the major sampling sites. The seaward boundary of the Tsitsikamma National Park is indicated by the solid line (x - site for mesh size comparisons; y - sites for day/night comparisons; z - sites at Middlebank and 5, 10 & 15 nautical miles for horizontal distribution study; * - sites off the Elands and Bloukrans Rivers used for vertical distribution study).



bongo tows. The majority of these were performed from *Natpark Aonyx*, but those in November 1993 and November 1994 came from the R.S. *Algoa*, while some in October 1995 and April 1996 were performed during R.S. *Africana* voyages. Seasonal patterns were determined separately for samples from Middlebank and from all other sampled sites combined.

5. The sample stations for the study on the horizontal distribution of ichthyoplankton along an offshore transect were chosen along a line off Storms River mouth starting from 5 nm and extending out to 15 nm (Figure 1.2). Middlebank was chosen as an inshore station over high profile reef. These locations were closest to the launching site and were chosen to cut down on travel time and boat running costs. All sampling was performed from *Natpark Aonyx*. Depth readings from the boat's echo-sounder revealed a range from 109-113 metres at 15 miles, 100-102 metres at 10 miles, 97-98.8 metres at 5 miles, and 23-60 metres on Middlebank. Sampling commenced in January 1995 and was terminated after May 1996. No samples were obtained in May 1995 (due to adverse weather conditions), September/October 1995 (*Africana* voyage #131), December 1995 (boat time not available due to peak holiday season) and April 1996 (*Africana* voyage #135). Due to logistical constraints and unpredictable weather, the 15 mile station was excluded from the program after the first three sampling trips.

6. All work concerned with the vertical distribution of ichthyoplankton was performed from the R.S. *Africana*. Site selection for samples obtained during research voyages were based on convenience, because ichthyoplankton sampling was never the primary objective during any of the voyages. South coast biomass surveys, performed by research ships belonging to the SFRI, were initiated in 1986 and trawling stations were assigned to 5 x 5 nm blocks on a semi-random basis (Badenhorst & Smale 1991). The aims of these surveys are outlined in more detail by Badenhorst & Smale (*op. cit.*), but generally deal with biomass, biology and faunal relationships of juvenile and adult commercial trawl species. Sample times had to fit in with other activities on board which enjoyed priority, and sample sites were chosen as the closest points in the reserve to the next designated site for trawling or hydroacoustic activity.

Discrete depth sampling was performed using the RMT 1x6 multiple opening and closing net system on two separate occasions while on board the R.S. *Africana*. Time was made available on

two consecutive nights, namely 7 and 8 October 1995 during voyage #131. On each day an inshore station off Elands River was sampled at around sunset (18h00) and an offshore site, also off Elands River (Figure 1.2), was sampled on three occasions at two hourly intervals (21h00, 23h00 and 01h00). The depth at the inshore site ranged from 39 to 42 metres, while offshore it varied between 93 and 102 metres. At each time and site two replicate tows were performed. Due to mechanical problems with the firing mechanism, only three nets could be used during each tow. Where possible the physical parameters of dissolved oxygen (DO), salinity, nitrate, nitrite, silicate, phosphate and chlorophyll *a* were measured at discrete depths with the ship's Conductivity, Temperature and Depth (CTD) rosette sampler.

On the second occasion, sampling was performed off Bloukrans River mouth (Figure 1.2) on 25 and 26 April 1996 during voyage #135. Water depth ranged from 62 to 71 metres. Discrete depth sampling was once again restricted to three strata. Replicate tows were performed at sunrise, midday, sunset and midnight on the 25th and sunrise, sunset and late night (10h30) on the 26th. Midday samples on the second day had to be forfeited to fit in with the trawling schedule and midnight samples had to be moved to an earlier time so that distant trawling grounds could be reached by the following morning. Where possible CTD profiles accompanied samples, but no salinity values were obtained during this voyage.

7. As a part of the preliminary assessment of the potential for dispersal by ichthyoplankton, satellite-tracked current-following drifters in the form of sub-surface "holey sock" canvas drogues (Colin 1995) eight metres in length and 60 cm in diameter, were released at fixed distances offshore in the morning and then recovered some time later that day. Drogues were attached to a large surface buoy so that they hung between three and eleven metres. An aluminium mast which housed a radio transmitter and battery pack protruded roughly 2 metres above the buoy. Location and recovery of the drogues was facilitated using a direction finder. The position of the drogues was recorded every minute on a Global Positioning System (GPS) mounted in a water-tight container on the mast above the water line and the track data was downloaded onto computer after each recovery. Release points were fixed along a line off Storms River mouth starting from one nautical mile offshore, while recovery points were totally reliant on current velocity and direction for that day. No drogues were left out overnight for fear of losing them. A total of 57 drogues were tracked between April 1996 and January 1997. For the purpose of this study, only the release and

recovery points were considered, and the straight line distance covered was calculated. Small scale meanderings of the drogue due to the effects of swell and tides were not incorporated here but will appear at a later stage (Colin Attwood, SFRI, Unpublished Data). Wind direction and velocity were estimated at the time of release and recovery. On two occasions during July and October 1996 replicate oblique bongo tows to a depth corresponding to the position of the drogue were performed at the sites of release of two of the drogues.

Current velocities and vectors were obtained at different depths using the Acoustic Doppler Current Profiler (ADCP) at several of the sample sites on consecutive days during the two R.S. *Africana* voyages. During voyage #131 readings were obtained inshore and offshore after sunset on both days, while profiles were obtained at sunrise, midday, sunset and midnight on the first day during voyage #135, but only at sunset and midnight on day 2. Although the ADCP measures currents with good vertical resolution in the upper 200 metres (Boyd & Shillington 1994), readings too close to the surface or the substrate are not possible because of interference (Alan Boyd, SFRI, Pers. Comm.). As a result of this, readings started at 18 metres during voyage #131 and 12 metres during voyage #135.

Additional details regarding gear types and sampling procedure as well as statistical analyses are dealt with in the appropriate chapters.

Ichthyoplankton Terminology

No matter what aspect of fish early life history is being studied, the stages of development need to be subdivided and clearly defined based upon processes and events which shape each phase so that interdisciplinary communication can be facilitated. In the past, different names for the same stages and differential subdivisions have been used by scientists practising in different fields (Kendall *et al.* 1984) resulting more in confusion than cohesion. The problem can also be seen to have arisen from the simple fact that fish development itself is by nature diverse (Richardson 1980) and to expect one system of terminology to be applicable to all is whimsical at best. For the purpose of this study the nomenclature used by Kendall *et al.* (*op. cit.*) and Leis & Trnski (1989), which is based upon some earlier works of Ahlstrom & Ball (1954) and Moser & Ahlstrom (1970), was used. The three primary developmental stages recognised by these workers are egg, larva and juvenile, with the egg and larval stages being further subdivided into early, middle and late egg stages, and preflexion, flexion and

postflexion larval stages. In addition both sets of authors recognise a transformation or transition larva as being the link between postflexion larvae and juveniles. Due to the sometimes extreme rearrangement of pigment patterns during yolk absorption, Kendall *et al.* (*op. cit*) proposed a further transitional phase between the egg and larval stages called the yolk-sac larva. Leis & Trnski (*op. cit.*) appear to refute this as being too inflexible, as the yolk-sac may be present during preflexion, flexion and postflexion larval stages depending on the species. Similarly, while Kendall *et al.* (*op. cit.*) restrict settlement until after metamorphosis into the juvenile form, Leis & Trnski (*op. cit.*) state that settlement may occur during any stage from larva through to adult or not at all if a pelagic existence is pursued for an entire lifetime. Nevertheless, an amalgamation of the two approaches seemed able to contend with any eventuality which arose during the course of this study.

CHAPTER 2 - SAMPLING AREA AND MATERIALS & METHODS

INTRODUCTION

Pelagic larvae are the most common early life-history form in marine teleosts, but vast differences in larval size, morphology and behaviour complicate accurate sampling (Choat, Doherty, Kerrigan & Leis 1993). Factors such as sampling gear, sampling frequency, net avoidance, and vertical/horizontal migration will affect the estimation of density and distribution of plankton (Omori & Ikeda 1984b). Variation of plankton occurs spatially and temporally over a wide range, and may be the result of growth, reproduction, mortality, migration, or behaviour. The advective losses and spatial heterogeneity in density and distribution also contribute to variation. The pelagic larval phase is usually short lived, but is subject to high levels of mortality and is prone to dispersion. While eggs and larvae may occur in very high concentrations in patches (Sherman, Lasker, Richards & Kendall 1983) they comprise < 5% in number and volume of the total plankton (Richards 1985). In order to sample the entire size range of larvae to provide information on recruitment, an array of sampling techniques should be employed, all of which possess their own areas of bias in terms of numbers, sizes and identification of larvae collected. Ichthyoplankton surveys make use of plankton nets of varying shapes, configurations and dimensions which may be towed, pushed or held stationary (Gallagher & Conner 1983). The effectiveness of three towed nets (bongos, Tucker trawl and neuston net), one purse seine and two aggregation devices (light trap and a light-seine) were compared with respect to taxonomic composition of samples, patterns of density and abundance, size structure of component taxa, and temporal patterns in density over short periods (Choat *et al. op. cit.*). Their results showed conclusively that bongo nets collected the most families (including all the abundant ones) as well as the widest size ranges in most of these. The light trap produced fewest families and mostly only the larger individuals. The light-seine and Tucker trawl caught most of the abundant families, all having a good size range representation, while the neuston net and the purse seine captured the same abundant taxa and exhibited similar size range compositions. It was apparent from these results that taxonomic composition and quantity of larvae is heavily dependent on sampling methodology and gear type. The consistent high density estimates provided by bongos for small larvae reflect the low avoidance and high retention properties of this type of gear when fitted with fine mesh. Other studies (e.g. Clarke 1991) support the above findings that when larval densities are high, bongo nets are the most effective samplers of small and large larvae when compared to a large Isaacs-Kidd trawl, while

Nakamura (1994) found that bongos outperformed ring nets in terms of numbers and size of larvae. Smoother water flow in front of and throughout the array and a uniform flow rate is thought to explain their greater performance (Posgay & Marak 1980). Lastly, the two nets mounted from a single central yolk make bongos ideal for collecting a greater number of samples at a faster rate than a single ring net (Snyder 1983).

Variable environmental conditions ensure that egg and larval distribution is not uniform, and even in homogenous environments where water is not stratified, distribution is patchy (Snyder 1983). This observed patchiness presents statistical problems when attempting to estimate abundance because it is a major source of sampling error (Davis, Jenkins & Young 1990). In order to reduce such errors one requires a balance between the size of the gear, the sampling method (towing speed and time) and the scale of patchiness (Wiebe 1971, 1972 in Davis *et al.* 1990), as well as large numbers of replicates (Colby 1988). Interpretation of the data must take into account the patchiness or micro-distribution which characterises many fish eggs and larvae (Marcy & Dahlberg 1980; Gallagher & Conner 1983) as well as the sampling bias and inefficiency of the gear and the techniques used. When sampling, one must assume that the small volume filtered in the towed nets represents the whole volume of water in the study region (Omori & Ikeda 1984b). Long-term variations in composition and abundance of species in the plankton community of a particular region can be best estimated from a sampling strategy making use of a single type of gear and a standard operating procedure. Net samples allow for the measure of mean densities of animals over a large volume but do not measure density or distribution on smaller spatial scales.

Catch composition and catching efficiency using towed plankton nets are affected by loss of organisms due to extrusion, net avoidance and filtration efficiency - in turn affected by mesh size, body shape, open mouth area, pressure across the mesh and towing speed (Choat *et al.* 1993). Avoidance and escapement through extrusion, which affects catching efficiency, are both related (Munk 1988), with one being enhanced when the other is reduced. Filtration efficiency is a function of net size and design and all attempts should be made to maximise this. It is also important to note that factors such as vertical stratification can affect analyses because gear types sample different regions of the water column. Variation due to horizontal and temporal factors also play a role when the timing of sampling cannot be the same each time and where some gear is moved great distances (towed nets) and others remain static (light traps). It is a given that no single method can provide

sufficient data to answer all questions, but the financial and logistical constraints of many programs often preclude the use of a vast array of methods. One should always be aware of the limitations and applicability (to the situation at hand) of sampling gear and methodology and realise that the extent to which questions can be asked and answered depends on a combination of logistics, gear bias, taxonomic composition, size range of fishes caught and the physical conditions of the sampling environment.

Study Area

There are a total of 57 Marine Protected Area's (MPA's) along the South African coastline, the majority of which (27) are located in the western Cape and the fewest (2) in the northern Cape. Of these there are 13 marine reserves, 17 restricted areas (general and single species), four National Parks and 23 provincial MPA's (Attwood, Mann, Beaumont & Harris 1997). Despite the apparent abundance of MPA's along this coastline, it remains disturbing that only five of these are "no take" zones, while the rest offer only the bare minimum of protection for a few or single species. The Tsitsikamma National Park (TNP) has been defined as one of these no take zones, although a small section of the coast is open to shore fishing by visitors, a practice soon to be abolished by National Parks (Corrie Pieterse, TNP Warden, Pers. Comm.). Students and staff of the Department of Ichthyology and Fisheries Science at Rhodes University have long been involved in research within the TNP. Due to much of the required infrastructure already being in place, the TNP provided a good starting point for an investigation into the nearshore ichthyoplankton assemblage of the south eastern Cape. In addition, it was hoped that this work would assist future ichthyoplankton surveys to complement the long term monitoring program on the effectiveness of MPA's towards linefish conservation.

The Tsitsikamma Environment

The east and west coasts of southern Africa are characterised by different physical, chemical and biological features, mainly as a result of the warm Mozambique and Agulhas Currents which flow along the east coast and the cold Benguela Current which flows up the west coast as far as southern Angola (Shannon 1989). The waters of the eastern seaboard of South Africa are predominantly influenced by tropical Indian Ocean waters which are carried by the fast-flowing Agulhas Current. Further south, the influence of cooler waters which are part of the equatorward drift of South East Atlantic waters becomes stronger. Based primarily on the temperature regime

of the sea and using distributional patterns of representatives from sandy beach communities and algae, amphipods, hydrozoans and fish, the coast of southern Africa can be divided into three biogeographical provinces (Brown & Jarman 1978; McLachlan, Wooldridge & Dye 1981; Hockey & Buxton 1989). These are a cool west-coast temperate province, a warm south-coast temperate province, and a warm east-coast sub-tropical province, and they display transitional zones between them rather than distinct boundaries. However, with the overlap between east and south coast, and south and west coast provinces being Port St. Johns (Transkei) to Woody Cape (Port Elizabeth) and Cape Agulhas to Cape Peninsula respectively, the TNP lies firmly within the bounds of the warm south-coast temperate faunal province. A more recent approach (Emanuel, Bustamente, Branch, Eekhout & Odendaal 1992) of dividing the coast into zoogeographic provinces using distributional records of 2000 invertebrate species also places the study area comfortably within the warm temperate south coast province.

The region along the east coast between Cape Point and East London is dominated by a roughly triangular extension of the continental shelf known as the Agulhas Bank, which measures 250 km wide at its apex and covers approximately 116 000 km^2 (Boyd & Shillington 1994; Hutchings 1994; Probyn, Mitchell-Innes, Brown, Hutchings & Carter 1994). Whereas the continental shelf-edge roughly follows the 200 m depth contour along the east coast, it deepens on the west coast to 400 m such that a large proportion of the shelf is considerably deeper (Hutchings *op. cit.*; Roberts & Sauer 1994).

The Agulhas Current is typical of other western boundary currents around the world (Harris 1964), such as the Gulf Stream or Florida Current in the North Atlantic, the Brazil Current in the South Atlantic, and the Kuroshio off Japan in the North Pacific. It extends below 1 000 meters, exhibits speeds in excess of 2 m.s^{-1} in the core (Gründlingh 1980), has a volume flux measured between 40-70 x 10^6 m^3.s^{-1} (Boyd & Shillington 1994), and closely follows the edge of the continental shelf (Shannon 1970; Gründlingh & Lutjeharms 1979) which lies between 90 and 100 km offshore in the Tsitsikamma region (Schumann & Beekman 1984; Tilney, Nelson, Radloff & Buxton 1996). While the current flows close to the coastline further north and has significant influence on both climate and oceanographic conditions (Lutjeharms & Connell 1989; Lutjeharms, Grünlingh & Carter 1989), its effect on the nearshore zone in the south-east Cape is less obvious. Currents in these south coast neritic waters are influenced by the coastline's bathymetric orientation in relation to the predominantly east-west winds (Harris 1978; Schumann, Ross & Goschen 1988;

Lutjeharms & Stockton 1991; Boyd & Shillington 1994; Jury 1994; Roberts & Sauer 1994) such that the whole system has been designated a wind-forced inner shelf region (Largier, Chapman, Peterson & Swart 1992). These longshore currents typically have surface speeds of around 25 cm/s^{1} (maximum of 50 cm/s^{1}), bottom speeds < 10 cm/s^{1}, and exhibit a cycle of reversal with a periodicity around three days (Boyd, Taunton-Clark & Oberholster 1992; Tilney & Buxton 1994; Tilney *et al. op. cit.*), although Jury (*op. cit.*) states that it may also be irregular, between 2 to 20 days. This meso-scale variation most likely originates from sea level disturbances resulting from the formation and passage from west to east of coastal-trapped low-pressure cells and their associated coastal trapped waves (CTW) emanating from eastward moving anti-cyclone weather features (Schumann 1989; Schumann & Brink 1990; Schumann 1998). These features generate winds orientated along the east-west plane parallel to the coastline (Schumann 1987), and generally have a periodicity of between five and nine days and propagation speeds between five and nine m.s^{-1}, causing nearshore current reversals from east to west (Schumann & Brink *op. cit.*) with a time lag of around one day (Tilney *et al. op. cit.*).

During the summer months the nearshore thermocline is very pronounced and the water column is dominated by surface stratification and a deep mixed layer. The reverse situation is evident in winter when storms and their accompanying westerly winds erode the thermocline resulting in mixing and a more or less isothermal deeper upper-layer (Schumann & Beekman 1984; Boyd, Tromp & Horstman 1985; Hanekom, Hutchings, Joubert & van Der Byl 1989). One of the most remarkable oceanographic features during the summer months is the localised, sporadic wind-induced upwelling (Schumann, Perrins & Hunter 1982; Hutchings 1994; Roberts & Sauer 1994). The eastward movement of upper atmospheric Rossby waves controls the passage of high and low pressure cells across the region (Jury 1994). When the high pressure cell moves past to the south, easterly winds predominate, and when these winds blow with enough force and for long enough they combine with the topography of the bays to the east of prominent capes to induce offshore Eckman transport which results in upwelling (Walker 1986; Jury 1988; Schumann, Ross & Goschen 1988; Hanekom *et al. op. cit.*). Cold waters beneath the thermocline are pushed upwards, first raising the level of the thermocline and then disrupting it (Mitchell-Innes 1988) as cool waters well up from the depths against the coastline. These bottom waters are rich in nutrients and as they are pushed into the photic zone conditions are optimal for phytoplankton blooms, the trigger mechanism of the planktonic food chain. The closest cape and bay to Tsitsikamma, Cape St

Francis, experiences strong upwelling events, mostly between November and May when easterly winds dominate the synoptic pattern (Hanekom *et al. op. cit.*). Upwelled water moves westward and offshore and may extend up to 80 km west of Cape St Francis (Schumann *et al.* 1982) as far as Storm River. A short term data series of wind velocity and vectors related to water temperature at selected depths appears in Figure 2.1. Wind data is from the remote weather station at Storms River and temperature readings come from an array of probes which was moored off Storms River mouth in 43 metres of water (Schumann In Press). The relationship between easterly winds and sudden drops in temperature are evident as are the corresponding temperature increases which coincide with westerly winds which reverse the whole process by causing downwelling and the net onshore movement of warm surface waters (Schumann *et al.* 1982; Beckley 1983). This oceanographic phenomenon of upwelling represents one of the most prominent determining factors when it comes to ichthyoplankton distribution (Parrish, Nelson & Bakun 1981; Sanchez-Velasco & Flores-Coto 1994), as spawning habits of adult fish must be compatible with regional patterns to ensure survival (Moser & Smith 1993; Olivar & Shelton 1993). For example, the two clupeoid species *Opisthonema oglinum* and *Sardinella aurita* spawn over the neritic region of the Yucatan Shelf in the Gulf of Mexico during the trade wind induced upwelling in spring so that larvae can take advantage of the resultant abundant planktonic populations (Sanchez-Velasco & Flores-Coto *op. cit.*).

At most localities on the shoreward side of the Agulhas Bank easterly winds predominate in summer while west winds are more dominant in winter months (Harris 1978; Schumann 1992; Hutchings 1994). At Cape St Francis, westerly winds occur with a frequency of approximately 50% throughout the year (Hunter 1987 in Jury 1994), but easterlies increase to a peak of around 30% in summer. The mean wind velocities, dominant directions and strongest winds as well as a measure of calm periods for all available months of the duration of the project appear in Table 2.1. Measurements for these were obtained from the remote weather station at Storms River mouth. Both the dominant and strongest winds were clearly N, NNE, NE, ENE, E, SSW, SW and WSW, while ESE, SE and SSE were most frequently absent. There does not appear to be a clear pattern of easterly dominance in summer and westerlies in winter, with both appearing during most months. Top wind speeds of up to 23.7 $m.s^{-1}$ in October 1995 were mostly SSW, SW or WSW, with easterlies featuring only a few times. A slight seasonal trend was evident with respect to mean speeds which ranged from a low of 1.6 $m.s^{-1}$ in April 1996 to a maximum of 3.21 $m.s^{-1}$ in October

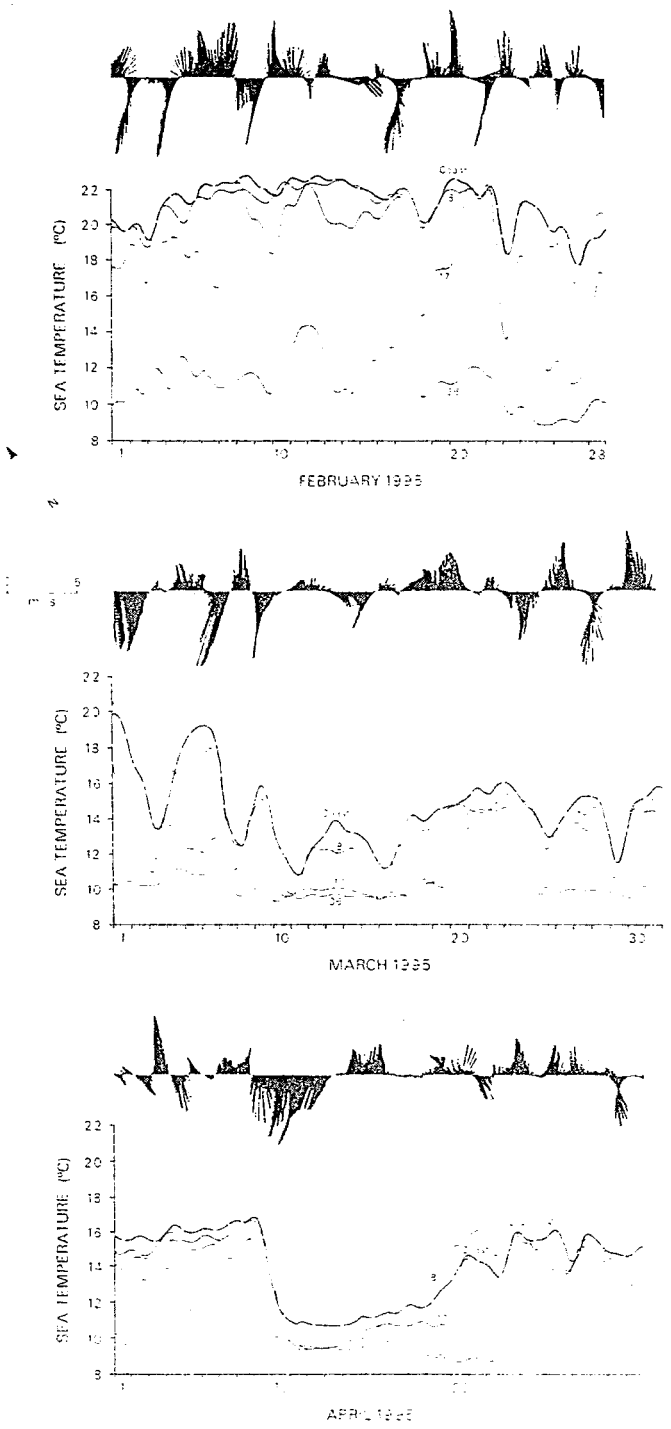


Figure 2.1 - Wind velocity ($m.s^{-1}$) and vectors with corresponding sea temperatures (°C) from the surface (coast) and 8, 17 & 36 meters, measured near Storms River mouth from February to April 1995 (from Schumann In Press).

Table 2.1 - Wind data gathered from the remote weather station at Storms River for the period August 1993 to June 1997. Both mean wind speed and maximum gust are measured in $m.s^{-1}$, with standard deviation of the mean speed in parentheses. Data are from the remote weather station at Storms River, and for certain months (e.g. March 1997 - June 1997) only limited readings were made available.

Year	Month	Mean Speed ($m.s^{-1}$)	Maximum gust ($m.s^{-1}$)	Dominant winds	Strongest winds	Absent	% Calm
1993	August	2.3 (1.21)	16.4 ESE	SSW, W, E, NE	ESE, E, SSW	SSE	19.7
	September	2.1 (1.32)	15.8 SSE	No Data Available	No Data Available	No Data Available	22.8
	October	2.9 (1.28)	14.5 WSW	E, W, WSW	E, WSW	SSW, S, SSE, SE	21.5
	November	2.8 (1.04)	14.9 W	NE, E, W, WSW	ESE, E, WSW	SSE	19.3
	December	3.0 (0.95)	21.4 WSW	E, NE, WSW, W	E, W, SSW	No Data Available	15.8
1994	January	2.4 (1.32)	13.4 E	E, WSW	E, WSW	NW	28.7
	February	2.2 (1.1)	14.3 W	E, W, WSW	E, WSW	S, SSE, SE, NW, NNW, WNW	32.7
	March	2.2 (1.39)	13.4 E	NE, E, WSW	E, WSW	SE, SSE, NW	3
	April	1.9 (1.08)	16.7 W	NE, E, WSW	E, W, WSW	SE, SSE, S	34
	May	1.9 (0.86)	18.6 W	NE, W, WSW	E, WSW, W	SSE, SE	27
	June	2.2 (1.13)	21.1 WSW	N, NE, WSW, W	W, WSW	E, ESE, SE, SSE	26.9
	July	2.3 (0.91)	17.8 WSW	N, NE, WSW, W	N, E, S, SSW, SW, WSW, W	ESE, SE, SSE	21.3
	August	2.4 (1.1)	20.3 WSW	N, NE, E, WSW, W	NE, E, ESE, SE, WSW, W	SSE	21.1
	September	2.6 (1.01)	21.2 WSW	N, NNE, NE, E, WSW, W	E, WSW, W	SE, SSE	18.1
	October	2.3 (0.92)	15.3 S	N, NNE, NE, E, S	N, NE, E, S, WSW	No Data Available	22.8
	November	2.7 (1.3)	20.6 SSW	N, NE, S, SSW, NW	NNE, NE, ENE, S, SSW, NW	WSW	16.2
	December	2.7 (1.13)	15.7 NE	N, NNE, NE, S	N, NNE, NE, ENE, E, ESE, S	No Data Available	21.2
1995	January	2.4 (0.9)	14.7 SSW	N, NNE, NE, ENE, S, SSW, NW, NNW	NNE, NE, ENE, S, SSW	No Data Available	23.2
	February	2.8 (0.88)	15.1 SSW	N, ENE, SSW, SW, NW, NNW	NE, ENE, SSW, SW	No Data Available	14.4
	March	2.2 (1.55)	19.0 SSW	ESE, SE, W, WNW, NNW	E, ESE, SE, SW, WSW, W, WNW	No Data Available	25.5
	April	2.1 (1.09)	16.0 SSE	No Data Available	No Data Available	No Data Available	26.7
	May	2.02 (0.95)	19.3 SW	SSW, SW, NW, N	NE, ENE, SSW, SW	ESE, SE, SSE	25.1
	June	1.9 (0.56)	19.8 SW	SSW, SW, NW, N	NE, ENE, SW, NW	E, ESE, SE, SSE	24.1
	July	2.55 (0.79)	21.6 SW	SSW, SW, NW, N	SSW, SW	NE, ENE, ESE, SE, SSE	14.5
	August	2.56 (0.92)	23.1 SSW	ENE, SSW, SW, N	ENE, SSW, SW	ESE, SE, SSE	16.3
	September	2.47 (0.74)	17.3 SW	SSW, SW, N	ENE, SSW, SW	SE	18.8
	October	3.21 (1.13)	23.7 SW	SSW, SW, N	SSW, SW	No Data Available	10
	November	2.91 (1.15)	18.1 SSE	SSW, SW, N	NE, ENE, SSW, SW	No Data Available	11.5
	December	2.86 (1.41)	16.2 NNE	NE, ENE, SW	NE, ENE, SW, NW	ESE, SE, SSE	20.8

Table 2.1 continued.

Year	Month	Mean Speed ($m.s^{-1}$)	Maximum gust ($m.s^{-1}$)	Dominant winds	Strongest winds	Absent	% Calm
1996	January	2.3 (0.74)	14.2 SSW	NE, ENE, SSW, SW, N	NE, ENE, E, SSW		24.4
	February	2.5 (1.27)	15.5 SSW	NE, ENE, SSW, SW, N	NE, ENE, E, SSW	ESE, SE, SSE	25.1
	March	2.3 (1.04)	17.8 SW	No Data Available	No Data Available		29.2
	April	1.6 (0.65)	15.7 WSW	No Data Available	No Data Available		39.3
	May	1.7 (0.8)	17.7 SW	No Data Available	No Data Available		33.6
	June	2.2 (0.79)	21.7 N	No Data Available	No Data Available		14.1
	July	2.7 (0.97)	21.0 W	No Data Available	No Data Available		14.1
	August	2.7 (1.07)	23.2 W	No Data Available	No Data Available		17.3
	September	3.0 (1.18)	24.4 W	No Data Available	No Data Available		12.4
	October	2.7 (1.1)	17.1 W	No Data Available	No Data Available		17.2
	November	2.8 (1.25)	19.8 W	No Data Available	No Data Available		14.4
	December	2.8 (1.3)	19.6 W	No Data Available	No Data Available		16.1
1997	January	2.9 (1.08)	18.4 W	No Data Available	No Data Available		9.4
	February	3.1 (0.83)	16.9 W	No Data Available	No Data Available		7.1
	March	2.5 (1.19)	18.5 W	No Data Available	No Data Available		22
	April	2.1 (1.04)	18.9 W	No Data Available	No Data Available		23.2
	May	2.1 (0.75)	17.0 W	No Data Available	No Data Available		21.9
	June	2.2 (0.64)	20.2 W	No Data Available	No Data Available		15.7

1995. Autumn and winter values were slightly lower than those for spring and summer. The percentage hours in each month during which no wind was registered was highly variable with no season exhibiting more calm weather than others. In some cases approximately a third of the month registered as calm, e.g. February 1994 (32.7%), April 1994 (34%), April 1996 (39.3%) and May 1996 (33.6%). At the other end of the spectrum, some months were extremely windy, with calm periods being measured for less than 10% of the time (Table 2.1), e.g. March 1994 (3%), October 1995 (10%), January 1997 (9.4%) and February 1997 (7.1%).

Historical data indicates that mean sea surface temperature is modulated quite consistently from year to year on a seasonal basis from 16 - 17°C in winter to 20 - 21°C in summer (Schumann & Beekman 1984; Greenwood & Taunton-Clark 1994). Monthly sub-surface temperatures from January 1991 to July 1992 (Tilney & Buxton 1994) conformed to this pattern, with autumn and winter mean temperatures only registering at 3°C colder than for spring and summer. The mean monthly sea temperatures for each year during this study from January 1994 to June 1997 and for all years combined are presented in Figures 2.2 and 2.3.

Over this 42 month period February had the highest mean temperature at 18.6°C, with July and August sharing the lowest at 15.5°C (Figure 2.2). True to form, a maximum of only 3.1°C separated summer and winter sea surface temperatures (SST). On a seasonal basis, winter appears to be the most stable with the least amount of variation. Only 0.5°C separates the mean temperatures and 6.3°C separates the lowest and highest recorded values. Although the mean monthly SST's for spring differ the most, the spread of temperatures are greatest in summer when upwelling activity is at its peak, resulting in observed temperature differences of 12.8°C (Figure 2.2).

On a yearly basis the variation is somewhat more emphasised. In 1994 (Figure 2.3), 4.9°C separated the highest and lowest mean SST's due to an abnormally high mean value in November. If this is excluded, only 2.1°C separates the maximum and minimum mean values. The wide range of SST's from October to March (maximum difference of 11.1°C in January) illustrates the duration and most intense period of the upwelling season. No values for April were available in upwelling and with a mixed water column. A stratified water column with a shallow, prominent 1995 (Figure 2.3), but once again winter was thermally the most stable season in the absence of upwelling and with a mixed water column. A stratified water column with a shallow, prominent

thermocline characterises the region toward the end of spring and in summer. It would appear, however, that upwelling was sporadic over this year, featuring only in January, March and December. Uncharacteristically high temperatures in February (a mean of 21.3°C and a maximum of 23.4°C) meant that 6.8°C separated the highest and lowest mean SST's. The upwelling season was more prolonged in 1996 with perhaps the most intense period yet observed in January when a 12°C drop in temperature bore testament to the force of this oceanographic feature (Figure 2.3). Spring was the season displaying the least variation with only 0.6°C between the mean SST's from September to November. The high mean temperature in December (19.8°C) marked the beginning of an unusually warm spell in the Eastern Cape which continued well into February of 1997 (Figure 2.3). Upwelling was absent in December 1996 and January 1997 with lows of only 16.8°C and 18.7°C being recorded respectively. February, however, was a month which started out with extremely warm waters but then experienced the effects of severe upwellings toward the end, with a temperature difference of 12.5°C between the highest and lowest values. The situation had reverted to the normal trend by March, and autumn and June temperature means and ranges were much like those recorded for previous years. An important point to consider is that while upwelling may occur it is at times not intense enough to cause a reduction in SST. Low intensity upwellings could cause decreases in sub-surface temperatures as the thermocline is pushed upwards but not as far as the surface.

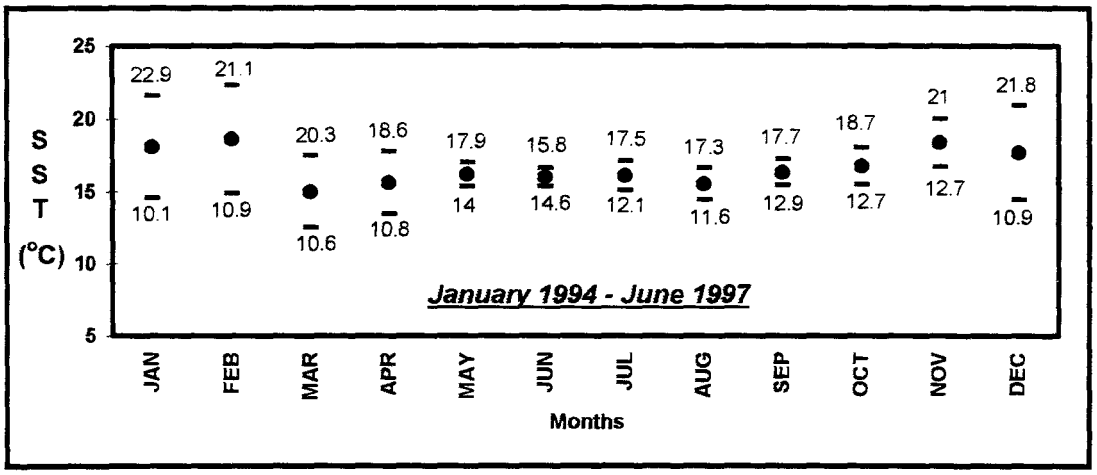


Figure 2.2 - Combined mean monthly sea surface temperatures (SST - °C), measured at Storms River from January 1994 to June 1997. The bars indicate the standard deviation and the numbers the maximum and minimum temperatures for each month.

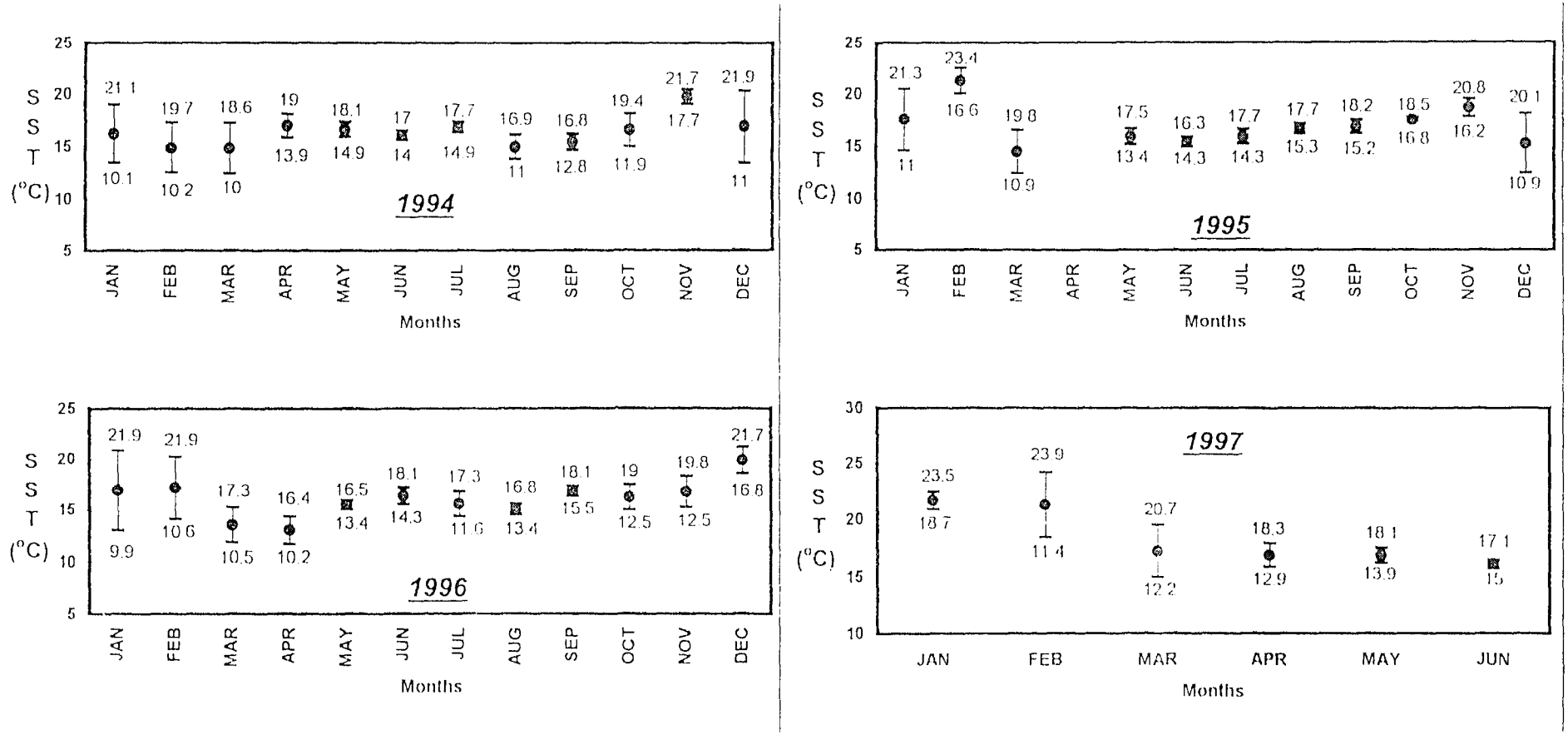


Figure 2.3 - Mean monthly sea surface temperatures (SST) in °C, measured at Storms River from January 1994 to June 1997. Each year is presented separately. Bars indicate the standard deviation and the numbers the maximum and minimum temperatures for each month.

A fairly recent addition to the oceanographic knowledge of the region was the discovery by Swart & Largier (1987) of a distinct sub-surface ridge of oceanically forced intrusions of cold water extending from the coastline between Mossel Bay and Cape St Francis in a south-westerly direction (Hutchings 1994), and centred over the 100 m depth contour (Walker 1986; Largier & Swart 1987). Evidence from CTD profiles and satellite imagery (temperature and pigment concentrations) indicate that this phenomenon is most prevalent in spring and summer (Hutchings 1992; Boyd & Shillington 1994) although when consulting historical records of oceanic patterns it was discovered that it could persist until as late as June in some years (Lutjeharms & Walters 1985). Further examination of historical data showed that its presence could also be variable, as it was strongly manifested between October 1985 and March 1986 and again in November between 1987 and 1989, but was weak in 1991 and seemingly absent altogether in 1990 (Swart & Largier *op. cit.*; Hutchings 1992; Peterson, Hutchings, Huggett & Largier 1992). The precise origin and dynamics of this feature are as yet not clearly understood as warm Agulhas water intrusions and wind mixing of surface layers have made its detection and study difficult (Boyd & Shillington *op. cit.*; Hutchings 1994). The surface and sub-surface cyclonic circulation which characterises this cool ridge (Swart & Largier *op. cit.*; Boyd, Taunton-Clark & Oberholster 1992) is the dominant feature over the central Agulhas Bank between Mossel Bay and Cape St Francis (Hutchings *op. cit.*). The offshore south-westward flow and the reverse eastward flow along its inner margin would tend to act as a large return mechanism for eggs and larvae such that they are retained over the central Agulhas Bank region. It has also been proposed that its nearshore origin is as a result of cool water which is advected offshore during upwelling in the east from Cape St Francis to Cape Seal after strong easterly winds (Walker *op. cit.*; Boyd & Shillington *op. cit.*).

The constantly changing, dynamic environment described above which characterises the neritic waters of the south-east coast would almost certainly influence key events in the life history of the fish species found there. Species composition and community structure are determined by fish distributional patterns which are mostly determined by temperature regimes. Furthermore, the above factors linked to upwelling events could have far reaching ramifications when considering adult spawning habits and localities, the resultant productivity which could mean vast larval food and predator concentrations, severe temperature oscillations resulting in mass mortalities (Hanekom *et al.* 1989), and the net offshore displacement of surface waters from a dispersal point of view. The predominant and frequently reversing longshore wind driven currents as well as the

sub-surface cold water ridge over the central part of the eastern Agulhas Bank infringing into nearshore waters may also have as yet untold effects on ichthyoplankton dynamics. The region is notorious for weather and seas which can change from calm to extremely rough in a matter of minutes. The high energy nature of the nearshore region is well known (Burger 1990) and often sampling times and duration have had to be adjusted for safety reasons.

SAMPLING PROCEDURE

Bongo Nets

The majority of samples were collected using 57 cm diameter bongos (McGowan & Brown 1966 in Choat *et al.* 1993; Posgay & Marak 1980) fitted with 3.9 meter long 505 micron (μ) mesh plankton nets and a centrally mounted General Oceanics 2030R6 flowmeter with a six digit counter in the right hand bongo frame to measure the volume of water filtered. A small adjustable stainless steel depressor was welded to the central yolk and angled forward to provide downward force during towing. Cod-ends fashioned from 10 mm diameter PVC pipe fitted with perspex bottoms and with 505μ mesh windows (Snyder 1983) were attached to the net ends by bolts and wing-nuts for easy removal. For the most part, these nets were towed behind the Parks Board patrol boat *Natpark Aonyx*, a 21 foot ski-boat with approximately 5 m^2 of working deck space, fitted with two 175 horse-power outboard engines. On two occasions bongo samples were collected from the R.S. *Algoa*. Although the dimensions of the array were the same as above, the net configuration for the mesh size comparisons was different with a 333μ mesh net on the left frame and a 505μ net on the right. On two further occasions bongo samples were collected during research voyages on board the R.S. *Africana*, where both nets were 505μ mesh. In all cases during research voyages, double oblique tows to within a few meters of the bottom were performed mechanically using a winch and all data regarding net dynamics, depth, temperature and volume filtered were logged electronically on the ship computer during the tow. More details about these tows appear in the relevant chapters.

Before field trials could be performed using the ski-boat, the flowmeters were calibrated and several aspects relating to net dynamics determined. The nets were cylinder-cones, with the front cylindrical section having an area of 1.81 m^2 while the rear conical section measured 2.79 m^2, giving a total net area of 4.6 m^2. The ratio of the total open area of mesh openings through which

water is filtered to the area of the mouth of the net (the open-area ratio - R) was calculated using the following equation (Omori & Ikeda 1984b):

$$\mathbf{R = aP/A}$$

where a is the total net area, P is the porosity or mesh size, and A is the mouth area. A net should have an R-value of at least 3.5 and preferably greater than 6 (Omori & Ikeda *op. cit.*). In the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program, nets are designed to ensure an R-value of between 8:1 - 15:1 (Posgay & Marak 1980). The 505 micron mesh nets in this study had an open-area ratio of 9.11:1. The combination of the cylinder-cone net design and the high R-value make bongos highly resistant to clogging under normal circumstances (Posgay & Marak *op. cit.*; Snyder 1983). High concentrations of filamentous algae or invertebrates such as ctenophores and salps would, however, cause clogging. This was observed first hand on several occasions during the course of this study.

The calibration of flow meters and calculation of filtration efficiency took place in a 33 metre swimming pool. Readings over a known distance were taken first with the bongo frames alone and then with the nets attached. Ten replicate tows were performed in each case, with the calibration calculations being based on the mean number of flow meter revolutions indicated on the digital display from the tows with nets attached and the volume of water filtered (V) which was calculated using the following equation:

$$\mathbf{V = \Pi r^2 \times L}$$

where Πr^2 is the mouth area of the bongo and L is the length of the swimming pool. Two flowmeters were calibrated at 86.15 and 87.72 counts per cubic meter of water passing through the mouth opening. The filtration efficiency of the gear (volume of water filtered by the nets divided by the volume of water presented to them), was calculated to be 94.72% and 95.73% from the two different flowmeters. Flowmeters were recalibrated at least once every three months.

In order to determine the relationship between length of tow rope and the depth of the bongo sampler, two methods were used. Firstly, depth gauges removed from SCUBA diving sealed pressure gauge (SPG) units were placed in the cod-ends and the indicator which recorded depth zeroed. Known lengths of rope were attached to the gear and let out while the boat maintained a steady towing speed around two knots off Storms River mouth. Upon recovery of the nets the maximum recorded depth was noted. Readings from the same length of rope were found to vary by

as much as 4.5 metres, most likely as a result of the different degrees of pressure resulting from water flow through the net and so this method was rejected in favour of the second. This involved a more direct approach where once the desired length of rope was out, a SCUBA diver equipped with two depth gauges would be dropped from the moving boat and descend rapidly until the nets were sighted. As the nets passed by, the diver would consult the depth gauges. This was repeated four times for each length of rope and the results of these observations are presented in Table 2.2.

Table 2.2 - The relationship between tow rope length and depth of Bongo nets determined during field trials off Storms River mouth, August 1993.

Rope out (m)	Mean depth (m)	Deviation
10	2.1	0.42
20	3.8	0.24
30	6.2	0.33
40	10.3	0.21
50	13.4	0.16
60	15.6	0.35
70	18.5	0.23
80	23.4	0.12
100	31.2	0.28

Except where indicated, all bongos performed from *Natpark Aonyx* were carried out with 70 metres of tow rope, i.e. a maximum depth of 18.5 ± 0.23 metres was sampled. This was due to the high profile reef in the area which rose up to 23 metres in places (a safety margin of around five metres from the shallowest point was chosen), and time and effort required to manually haul in the line after each tow. Depth would obviously be a function of towing speed, but confidence in the estimates was high as towing speed was standardised as close to two knots (kn) as possible.

Field Trials of Bongo Nets

All tows performed from *Natpark Aonyx* were double oblique hauls. Due to the lack of mechanical devices such as winches on board, a method had to be devised which would allow for the efficient paying out and retrieval of line by hand. A piece of mountaineering equipment known as a figure-of-eight (F-8) was attached to the stern of the boat by a bridle and a small, two litre volume buoy which kept the line on the surface and away from the propellers. The F-8 is designed to withstand loads of up to four tonnes and was presumed to be more than capable of holding up to the strain resulting from the towed nets. Jossi & Marak (1983) state that wire tension while towing 61 cm bongos is around 250 kg under normal circumstances, going up to a maximum of 1 000 kg

under dynamic loads. The towing rope, 10 mm braided sailing rope, was thread through the F-8 before being attached to the central yolk of the bongo frame by a D-shackle.

To prevent damage of the nets by the propellers, the starboard engine was used to bring the boat up to the desired towing speed and then the nets were lowered over the port side. Once clear of the boat, the port engine was then engaged for the duration of the tow. By keeping tension in the rope it was possible to feed it out through the F-8 at a constant rate, approximately 40 $cm.s^{-1}$. According to the guidelines provided by the MARMAP program (Jossi & Marak *op. cit.*) towing speed should ideally be between 1.5 and 2 kn with variations not to exceed 0.25 kn. A constant, conservative towing speed is important for several reasons, namely so that the nets sample equal volumes at all depths, so that avoidance, extrusion and sample damage are kept to a minimum, and so that long term comparable data are provided for the entire program. While a towing speed of around two knots was adhered to whenever possible there were deviations depending on the direction of towing relative to swell size and direction. For short periods during each tow, speed was retarded when the boat's direction was into the swell and increased when towing with the swell. Once the desired length of towing rope was out a large surface marker buoy with a cone-shaped, canvas drogue attached was clipped onto the tow line behind the F-8 and released. The buoyancy and drag combined with the forward motion of the boat meant that as this array moved back along the tow rope, the nets were brought to the surface. As soon as the nets were sighted on the surface the boat was turned and the nets pulled in by hand. The nets were stationary in the water at this time, hanging down limply, and even when they sank a couple of metres they were considered not to be sampling. Contamination during this retrieval period was assumed to be minimal. The nets were lifted over the side of the boat and washed down with a hand operated bilge pump mounted at the stern of the boat. The cod-ends were carefully removed and sea water allowed to drain from the mesh windows until the sample could be transferred to one litre plastic bottles. Each tow was timed from the moment the nets entered the water until they were seen on the surface. Flowmeter readings were taken prior to the nets going over the side and as soon as they were back on board and the filtered water volume calculated from the calibration values determined earlier.

Because larvae have been known to be stratified with depth, oblique bongo hauls must be highly accurate to ensure that the sample is representative of all depths combined (Munk 1988), e.g. a faulty retrieval can cause over-representation of a certain depth interval. It was assumed that

all depth layers were sampled equally provided that no entanglements of the towing line occurred and net deployment and recovery were without mishap. Gallagher & Conner (1983) stressed that one should be acutely aware of the sampling bias of the gear prior to interpreting the data. In terms of logistics, bongo nets were the most feasible option, and although it is recognised that they are amongst the most efficient samplers (Choat *et al.* 1993) it was realised that smaller and large post-flexion stages could be under-sampled due to extrusion and avoidance respectively.

RMT 1x6

The RMT 1x6 is a multiple opening-closing array fitted with six 333μ mesh nets capable of sampling at discrete depths with virtually no contamination. As a result of the size of the apparatus, each net has an effective mouth area of 1.414 m^2 and it requires a 40 kg bar weight for stabilisation and downward force. it can only be operated from large vessels with power winch capabilities. All RMT sampling was performed on the R.S. *Africana*. An attempt was made from the R.S. *Algoa*, but faulty electronic equipment meant that the procedure had to be aborted.

All control is from the surface, and sensors on the net provide real time data on a computer monitor which allows for the opening and closing of nets at desired depths through a conducting cable. All relevant data is logged on the computer and includes volume sampled at each depth and a depth/temperature profile recorded by means of an electronic bathythermograph. No cod-end buckets are used on the research ships, instead the net ends are doubled back and tied shut with cord. While this provides an excellent seal, there is the danger of damage to specimens through abrasion against the mesh under pressure which merely serves to compound the problems already associated with identification. Logging of data starts as soon as the nets are lowered into the water and is terminated when they reach the surface again. The RMT is lowered using a wire-out speed of 1 $m.s^{-1}$ with the bottom net opened for stabilisation. When the net reaches to within 5 - 10 metres from the bottom the first sampling net is triggered and retrieval starts with a wire-in speed of 0.5 $m.s^{-1}$. Subsequent nets are triggered when the trace on the monitor shows them to be at the desired depths. The lag time between triggering from the surface and the firing of the pin to release the net is about three seconds. The slow retrieval speed and angle of wire-out mean that contamination is minimal. Once on deck a high pressure hose operated from the ship's pumps was used to wash the nets down. The tied ends were opened over large 25 litre plastic buckets and the

sample washed out. The bucket contents were then filtered through 333μ mesh sieves and poured into one litre plastic bottles.

Sample Fixation and Preservation

The violent reaction and contortions exhibited by live specimens when they come into contact with a fixative like formalin can result in undue breakages and distortions (Omori & Ikeda 1984c) which could complicate identification and measurement. To prevent this, fish larvae were exposed to a muscle relaxant before fixation by sprinkling a few Menthol Crystals (Saarchem [PTY] LTD) on the surface of the sample. Once they had dissolved and the larvae showed no reaction to a touch stimulus (± 45 minutes), concentrated buffered formalin was added to make up an estimated 5% by volume solution. Because the fixatives and preservatives commonly used bleach out pigments fairly quickly (Leis & Rennis 1983), a small amount of a 40% emulsifiable concentrate of a phenolic antioxidant, butylated hydroxytoluene (BHT - ICN Biochemicals, Inc.), was added to each sample (see Snyder 1983). According to Omori & Ikeda (*op. cit.*) a reasonable degree of pigmentation can be preserved for up to a year using this method. After two weeks in the 5% formalin fixative, samples were transferred to a 70% propyl alcohol solution - although ethanol is the preferred preservative, its cost prevented its use here. Eggs and larvae were rinsed in distilled water to remove all traces of sea water prior to transfer into propanol to prevent a cotton-wool type precipitation from Calcium and Magnesium salts (Omori & Ikeda *op. cit.*).

Sample Identification and Processing

In the laboratory larvae were separated from the rest of the plankton with needles and fine forceps (#5 Inox) under 10 - 65x magnification on the stage of a Nikon SMZ-2T dissecting microscope. Eggs were either removed with forceps or a glass dropper. If two weeks had not yet passed since collection, eggs and larvae were placed into 5% formalin, otherwise they were stored in 70% propyl alcohol to await identification.

In spite of the many characters exhibited by eggs which may be used in their identification, the degree of certainty from field samples is very often low (Matarese & Sandknop 1984). Characters most often used include shape, size, oil globules, yolk, chorion, perivitelline space, embryonic features and miscellaneous characters such as secondary membranes, cleavage pattern, micropyle size and biochemical analyses. A process of elimination can also be used based upon the sampling gear used and the area sampled (Matarese & Sandknop *op. cit.*). In

many cases newly spawned eggs are not readily identifiable and in some cases identification is hampered because of size and appearance similarities to other species (Jossi & Marak 1983). Due to the poor status of egg systematics for the region and the time constraints on sorting samples, all eggs were grouped together with the exception of those belonging to *E. japonicus*, which are ovoid or elliptical as opposed to round and hence easily distinguishable.

Larvae were identified to the lowest possible taxon (species or family) with the aid of Melville-Smith (1978), Brownell (1979), Leis & Rennis (1983), Moser *et al.* (1984), Okiyama (1988), Leis & Trnski (1989), Olivar & Fortuño (1991), Davis & Buxton (1996) and from specimens collected during a preliminary ichthyoplankton survey of the TNP (Tilney & Buxton 1994). On a few occasions it was necessary to clear (trypsin) and counter- stain larger individuals with alcian blue for cartilage and alizarin red S for bone (Potthoff 1984; Taylor & Van Dyke 1985) to provide a better picture of skeletal and fin structure. This process was also used during the description and illustration of certain species and is dealt with in Chapter 4. Taxonomic nomenclature follows that of Smith & Heemstra (1986).

In all cases the body length (BL) of larvae was measured to the nearest 0.1 mm with a Nikon S10x micrometer eyepiece which had been calibrated against a pair of Mitutoyo® vernier calipers. The body length used for pre-flexion and flexion larvae was notochord length (NL) and corresponded to the distance from the tip of the snout to the posterior tip of the notochord, while body length in postflexion and recently metamorphosed juveniles was standard length (SL) which corresponded to a length from the tip of the snout to the posterior edge of the hypural plate (*sensu* Leis & Rennis 1983). All samples are presently stored in 70% propyl in 14 ml McCartney glass bottles.

Measurement deviations, usually in the form of shrinkage and weight loss in larval and juvenile fish after fixation in formalin and preservation in alcohol has been reported for both freshwater and marine teleost species (Stobo 1972; Lockwood 1973; Theilacker 1980; Billy 1982; Hay 1984; Jennings 1991; Treasurer 1992), while Blaxter (1971) and Theilacker (1978, 1980) also reported on shrinkage before death resulting from autolysis and osmoregulatory problems arising from damage and mucous loss from mechanical damage incurred during the collection process. Correction factors and compensatory models (e.g. Theilacker 1980) tend

to be either species specific or loosely compatible with other species in the same family, and based on the use of ethanol as a preservative, not propanol. Discrepancies are also a function of salinity levels and fixative concentrations in combination with storage procedure and fish length (Hay *op. cit.*; Fowler & Smith 1983). No measurements of fish larvae were taken before or during the first few days of fixation, and as such no correction factors could be applied. In an attempt to standardise measurements in this study, the fixation period was set at two weeks and measurements only taken after 4 months' preservation in 70% propanol.

All egg and larval numbers, from all samples irrespective of gear type, were standardised to numbers per cubic meter of water filtered.

Statistical Analysis

A variety of statistical methods were employed to discern patterns in the data. The Educational Institution Edition of STATGRAPHICS® Version 7.0 was used applying 2-sample analysis t-tests, 1-way and Multiple Analysis of Variance (ANOVA) with interactions where applicable, the Kruskal-Wallis test, tests for variance heterogeneity, and regressions. As a further aid and to enhance the visual presentation in places, the Plymouth Routines In Multivariate Ecological Research (PRIMER®) package Version 4.0 was used. The package works by reducing the complexities of community structures by presenting them as graphical images based upon similarity matrices (Clarke & Warwick 1994) reflecting biological relationships between samples. Formats used were Multi-Dimensional Scaling (MDS) and an Analysis of Similarity (ANOSIM) on groups determined *a priori* to graphical imagery. All data analysed by these statistical packages were transformed as $\sqrt{(x-1)}$ for Statgraphics and 4th root ($\sqrt{\sqrt{}}$) for PRIMER to reduce variance and down-weight the importance of the very abundant species so that less dominant, and sometimes rare species, played a role in determining the similarity between samples (Clarke & Warwick *op. cit.*). The $\sqrt{(x-1)}$ variance stabilising transformation is considered to be the best for data such as this, which has a Poisson distribution and which is to be analysed using the Statgraphics package (Dr. Sara Radloff, Department of Mathematics and Statistics, Rhodes University, Pers. Comm.). The effect of the $\sqrt{\sqrt{}}$ transformation is quite severe in weighting down the very abundant species (Clarke & Warwick 1994). When dealing with large data sets and certain analytical procedures, it has become acceptable to exclude those taxa comprising < 1% of the catch (see

Choat *et al.* 1993) because the effect it has on the outcome of the analysis is negligible. A similar protocol was followed during this study and those species excluded from analysis are mentioned in the relevant chapters.

Selection of the Main Monthly Sample Site

Five replicate oblique bongo tows were performed at each of the three sites described in Chapter 1 on 19 August 1993 between 10h00 and 15h30. With 80 metres of tow rope out a maximum depth of 23.4 ± 0.12 m was sampled (Table 2.2). Diel vertical migratory patterns of larvae may have influenced catch composition, but this was assumed to be negligible as in most cases much of the depth profile was being sampled. All samples were taken during daylight hours when illumination was judged to be similar, so that the effects of net avoidance due to visibility were the same at all sites. Tow times ranged from 12 to 15 minutes - although time taken for the rope to be let out was very similar between tows, retrieval time varied, presumably as a result of the direction of towing relative to swell and current patterns. Sea surface temperature was a uniform 16.5°C with a light (± 5 kn) NE wind and a small, regular 2 - 3 foot swell. Mean volume filtered per net at the three sites was 133.71 ± 13.56 m^3, 112.2 ± 7.87 m^3, and 150.81 ± 9.54 m^3 at Middlebank, Rheeders and Steilkop respectively. The total volume of water filtered from all three sites was 3 826.66 m^3.

A total number of 24 families were identified comprising 7 470 larvae and 10 737 eggs. By far the most abundant family was the Clupeidae which registered the highest values at all three stations. The sequence of dominance following the clupieds was unique to each site. At Middlebank the Carangidae were next most abundant followed by Sparidae, Cynoglossidae and Callionymidae. At Rheeders the carangids were also the next dominant group which preceded the Sparidae, Merlucciidae, and Gadidae. The pattern at Steilkop was Gobiesocidae followed by Carangidae, Sparidae and Blenniidae. Of the 22 families identified 17, 16 and 14 were represented in the catch from Middlebank, Rheeders and Steilkop respectively. In terms of total larval concentration, Middlebank was by far the most productive ahead of Rheeders then Steilkop, a trend which persisted even when the overwhelming influence of the clupeids was removed. The same order of dominance was observed in terms of egg concentrations. The other twelve families which made up the rest of the catch, but which comprised only a

minor percentage of the total were Engraulidae, Scombridae, Clinidae, Haemulidae, Triglidae, Zeidae, Ophidiidae, Serranidae, Soleidae, Myctophidae, Bythitidae and Apogonidae.

A 2-way ANOVA showed there to be no significant difference ($P > 0.05$) between samples in the left and right nets and between replicate tows at each site for eggs, all families combined, all families excluding clupeids and for each family analysed separately. When the prototype for the original Bongo sampler was tested (McGowan & Brown 1966, in Choat *et al.* 1993) samples from left and right nets also showed no significant differences. Looking at concentrations between stations, a 2-way ANOVA with interaction incorporating replicate tows and sites. Rheeders and Steilkop are similar and significantly lower than Middlebank in terms of total larvae ($F_{2, 117.335}$; $P < 0.05$ - Table 2.3). All three stations differed significantly from each other when the clupeids were removed and when considering egg concentrations. The results for the dominant families appear in Table 2.3. For the most part concentrations were greatest at Middlebank and least at Steilkop, and differences were mostly significant. The exceptions to this were the Gobiesocidae and Blenniidae which were present in significantly greater numbers at Steilkop, Merlucciidae which were more prominent at Rheeders, Gobiidae in higher concentrations at both Rheeders and Steilkop, and Gempylidae which featured equally at all sites. There appears to be interaction between tows and stations with the Sparidae, Gobiesocidae, Blenniidae, Gadidae, Carangidae, and Cynoglossidae (Table 2.3). This involved one or two tows at most, and the heterogeneity of variance measured by Cochran's C-test in these instances, even after data transformation, means this must be interpreted carefully.

The MDS analysis performed on PRIMER (Figure 2.4) shows three distinct groups which are separated by site location, with Steilkop (12-21) being closer to Rheeders (22-32) than it is to Middlebank (1-11). The pairwise tests performed in the one-way ANOSIM, however, revealed that all three groups were distinctly different (Table 2.4) with 0% levels of similarity being recorded. This provides an excellent example of larval patchiness (see Snyder 1983) and shows how the species assemblage can appear to differ on a micro-scale over a short time period.

Table 2.3 - Results of the 2-way ANOVA with interactions between sites and replicate tows from Middlebank, Rheeders and Steilkop performed as part of site selection on 19 August 1993 (* indicates a significant difference at the 95% level; # indicates P-values < 0.05 which denotes heterogeneous variance).

	F-ratio (Significance level)			Variance (Cochran's C)		
	Tow	Station	Interaction	Tow	Station	Significance
Clupeidae	2.002 (0.146)	77.722 (0)*	2.266 (0.082)			M >> R = S
Sparidae	2.723 (0.069)	33.653 (0)*	5.458 (0.002)*	0.001#	3.4 E-6#	M > R > S
Gobiesocidae	23.305 (0)*	196.070 (0)*	19.89 (0)*	0.006#	6.9 E-13#	S >> R > M
Gobiidae	1.027 (0.425)	3.7 (0.049)*	1.35 (0.293)			R = S > M
Blenniidae	0.622 (0.653)	5.894 (0.013)*	4.526 (0.006)*	0.4	0.008#	S > M >> R
Cheilodactylidae	0.732 (0.584)	6.233 (0.011)*	1.395 (0.275)			M > R > S
Gadidae	2.109 (0.13)	7.944 (0.004)*	3.928 (0.011)*	0.01#	0.0006#	M > R > S
Carangidae	5.042 (0.009)*	302.242 (0)*	3.055 (0.03)*	1.7 E-5#	1.9 E-6#	M >> R > S
Cynoglossidae	2.218 (0.116)	18.277 (0)*	4.323 (0.007)*	0.001#	0.09	M > R > S
Gempylidae	1.122 (0.383)	1.566 (0.241)	1.094 (0.418)			M = R = S
Callionymidae	0.615 (0.659)	7.147 (0.007)*	0.873 (0.56)			M >> R >> S
Merlucciidae	0.173 (0.949)	8.13 (0.004)*	0.959 (0.501)			R >> M >> S
Total Larvae	2.336 (0.103)	117 335 (0)*	2.278 (0.081)			M >> R > S
Total excl. Clupeidae	3.947 (0.022)*	189.477 (0)*	2.512 (0.059)			M > R > S
Eggs	1.641 (0.216)	272.796 (0)*	2.266 (0.082)			M >> R > S

These trials for site selection and sampling procedure were terminated after a single day, partly because the technique had been perfected, but also due to the proximity of two of the sites to shallow waters which were deemed a hazard. Although the overall pattern of higher egg and larval abundance and the richest family representation at Middlebank led in part to it being chosen as the main study site, it was primarily as a result of safety that Steilkop and Rheeders were excluded. It was thought prudent to avoid these two sites because of their proximity to the shore and their shallower profiles which would make sampling in rougher seas impossible. In addition, the severe retroflection which results from wave action against the steep aspect of the littoral profile (Burger 1990) makes nearshore conditions unpredictable and hazardous. The shallow pinnacles at both sites and the blinders at Rheeders, determined to be potential fouling hazards for the nets, were to be avoided at all costs.

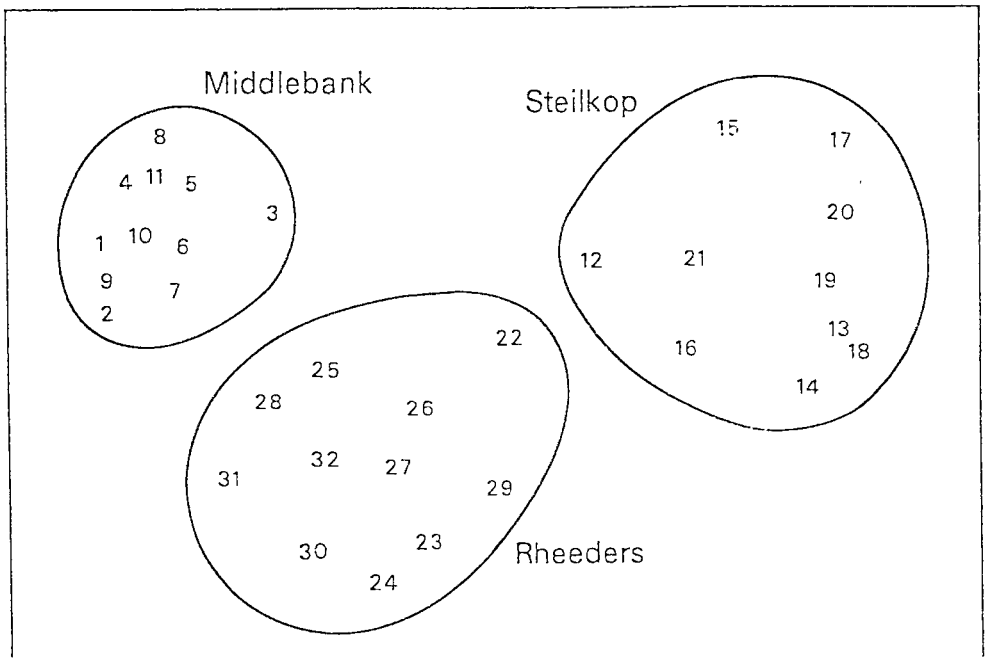


Figure 2.4 - The results of the Multi-dimensional scaling performed on the PRIMER package showing the distinct groupings from Middlebank (1-11), Steilkop (12-21) and Rheeders (22-32) from tows performed on August 19, 1993.

Table 2.4 - Results of the pairwise tests performed in the 1-way ANOSIM for samples from Middlebank, Rheeders and Steilkop collected as part of site selection on 19 August 1993.

		Pairwise tests		
Group	**Samples**	**Groups**	**Stat. value**	**Sig. Level**
Middlebank (1)	1-11	1 and 2	0.999	0.00%
Steilkop (2)	12-21	1 and 3	0.9	0.00%
Rheeders (3)	22-32	2 and 3	0.932	0.00%

Table 3.1 - Catch composition and egg & species concentrations (number of larvae or eggs per m^3 of water sampled) from three replicate bongo tows with different mesh sizes performed off Storms River mouth on November 24, 1993 during voyage #6 of the R.S. *Algoa*.

FAMILY	SPECIES	TOW #	LARVAL CONCENTRATION	
			505 microns	333 microns
Clupeidae	*Etrumeus whiteheadi*	1	0.068871	0.137741
		2	0.041386	0.056906
		3	0.034048	
	Sardinops sagax	1	0.103306	0.103306
		2	0.020693	
Engraulidae	*Engraulis japonicus*	1	0.241047	0.585399
Cynoglossidae	*Cynoglossus zanzibarensis*	1	0.068871	0.034435
		2	0.020693	0.005173
		3	0.068097	0.068097
Soleidae	*Austroglossus pectoralis*	1	0.034435	
		2		0.010347
		3		0.034048
Gobiidae	Species 1	1	0.034435	
		2	0.010347	0.010347
Gobiesocidae	Species 1	1	0.068871	
		2	0.005173	
Blenniidae	*Parablennius pilicornis*	1	0.034435	
		2	0.015520	0.015520
Sparidae	*Argyrozona argyrozona*	1		0.034435
		3	0.017024	
	Chrysoblephus laticeps	2		0.005173
	Spondyliosoma emarginatum	1	0.068871	
		2		0.005173
Triglidae	*Chelidonichthys capensis*	1		0.034435
Tetrarogidae	*Coccotropsis gymnoderma*	2	0.010347	0.020693
Callionymidae	*Paracallionymus costatus*	2	0.005173	0.025867
		3	0.017024	0.068097
Mugilidae	*Liza richardsoni*	2	0.005173	
Sciaenidae	*Atractoscion aequidens*	2		0.005173
Totals		1	0.929752	1.101928
		2	0.134506	0.165546
		3	0.136193	0.170242
		Total	0.217020	0.263270
Eggs		1	1.101928	1.480716
		2	0.770823	0.832902
		3	0.119169	0.340483
		Total	0.668849	0.796926

Table 3.2 - Mean size, size range and percentage flexion of the catch from three replicate bongo tows with different mesh sizes performed off Storms River mouth on November 24, 1993 during voyage #6 of the R.S. *Algoa*.

FAMILY	SPECIES	TOW #	MEAN SIZE (mm)		SIZE RANGE (mm)		% FLEXION	
			505 µ	333 µ	505 µ	333 µ	505 µ	333 µ
Clupeidae	*E. whiteheadi*	1	12.8 +- 0.71	13.43 +- 2.0	12.3 - 13.3	11.1- 15.5	100	50
		2	13.13 +- 3.22	9.83 +- 1.47	8.44 - 16.84	7.5 - 12.83	62.5	16.7
		3	13.51 +- 5.44		9.66 - 17.35		50	
	S. sagax	1	11.37 +-1.65	10.7 +-1.0	10.0 - 13.2	9.7 - 11.7	33	0
		2	11.61 +- 1.25		10.25 - 12.83		50	
Engraulidae	*E. japonicus*	1	8.16 +- 1.78	6.43 +- 2.3	6.55 - 11.2	3.8 - 10.9	28.6	11.8
Cynoglossidae	*C. zanzibarensis*	1	7.75 +- 0.35	5.3*	7.5 - 8.0		0	0
		2	6.48 +- 1.6	3.55*	4.4 - 8.3		75	0
		3	5.01 +- 3.14	3.09 +- 0.52	2.8 - 9.5	2.6 - 3.65	25	0
Soleidae	*A. pectoralis*	1	6.8*				100	
		2		3.02 +- 0.29		2.81 - 3.22		50
		3		5.5 +- 2.55		3.7 - 7.3		50
Gobiidae	Species 1	1	4.7*				0	
		2	3.4 +- 0	4.5 +- 0.14	3.4	4.4 - 4.6	0	100
Gobiesocidae	Species 1	1	3.12 +- 0.76		2.58 - 3.65		0	
		2	4.02*				0	
Blenniidae	*P. pilicornis*	1	7.65*				100	
		2	3.87 +- 1.44	6.92 +- 3.58	2.8 - 5.5	3.25 - 10.4	33.3	66.6
Sparidae	*A. argyrozona*	1		4.0*				0
		3	3.7*				0	
	C. laticeps	2		3.55*				0
	S. emarginatum	1	4.31 +- 0.78		3.75 - 4.86		0	
		2		4.5*				0
Triglidae	*C. capensis*	1		3.25*				0
Tetrarogidae	*C. gymnoderma*	2	5.53 +- 0.25	4.15 +- 0.49	5.35 - 5.7	3.8 - 4.5	100	0
Callionymidae	*P. costatus*	2	1.85*	2.7 +- 2.08		1.38 - 6.25	0	20
		3	2.65*	2.05 +- 0.84		1.5 - 3.3	0	0
Mugilidae	*L. richardsoni*	2	5.65*				100	
Sciaenidae	*A. aequidens*	2		3.55*				100

Day/night samples

Data pertaining to the filtered volume, number of eggs, number of fish and squid larvae, species richness and SST's for each of the stations sampled are presented in Table 3.3. Bottom temperatures and the position of the thermocline for stations sampled in November 1994, October 1995 and April 1996, and the results of the Kruskal-Wallis single factor ANOVA by ranks and the 1-way ANOVA tests applied to larval concentrations and sizes for each day also appear in Table 3.3.

Table 3.3 - Filtered volume, number of fish larvae, species richness, total number of eggs and *E. japonicus* eggs, and number of squid para-larvae sampled over Middlebank in March and August 1994, off Elands River in November 1994 and October 1995, and off Bloukrans River in April 1996. Included are SST's, with bottom temperatures and depth of the thermocline for October 1995 and April 1996 atations. Positive results of the Kruskal-Wallis single factor ANOVA by ranks and the 1-way ANOVA tests applied to data from each day also appear.

Date	Volume filtered (m3)	# Larvae	# Species	# Eggs	*E. japonicus* Eggs (#)	Squid		Water Temperature (°C) Time	Surface	Bottom	Thermocline Depth (m)	Statistics (all at 95% confidence level)
28/03/94	6579.74	22	7	8765				Sunrise	19	Not measured		H = 9.312 for higher conc. at midday compared to night for *C. gymnoderma*.
								Midday	19.2	Not measured		
								Sunset	19	Not measured		H = 10.271for combined larval sizes from each period, with midday larvae smaller than the rest.
								Night	19	Not measured		
29/08/94	2072.12	112	18	1024				Midday	17.5	Not measured		F = 18.279 & 91.57 for higher conc. at night for *E. whiteheadi* and *S. sagax* respectively.
								Night	18	Not measured		F = 7.489 for higher total conc. of larvae at night compared to midday.
												F = 9.998 for combined larval sizes from each period, with night caught larvae being larger.
03/11/94	3410.24	556	22	1696				Sunrise	18.7 - 18.9	11.5 - 11.7	12	H = 7.624 for higher conc. at sunrise for *P. costatus*.
								Midday	18.1	13.4	25 - 30	
								Sunset	18.3	13.8	25 - 30	H = 12.983 for smaller *E. japonicus* larvae from midday samples compared to sunrise.
												H = 28.129 for combined larval sizes from each period, with sunrise>midday>sunset.
7-8/10/95	1536.21	921	37	7609	5065	12	07/10/95	Sunset	17.5 - 17.6	9.8 - 9.9	40 - 55	F = 21.035 for higher conc. at midnight for *S. japonicus*.
								Midnight	18.4	10.9	35 - 50	F = 20.792 for higher conc. at sunset for *E. japonicus* eggs.
												F = 17.236 & 11.209 for larger larvae at midnight for *S. sagax* and Gobiidae Sp2 respectively.
												F = 8.617 for combined larval sizes from each period, with midnight larvae being larger.

Table 3.3 continued.

Date	Volume filtered (m3)	# Larvae	# Species	# Eggs	*E. japonicus* Eggs (#)	Squid		Water Temperature (°C) Time	Surface	Bottom	Thermocline Depth (m)	Statistics (all at 95% confidence level)
7-8/10/95							08/10/95	Sunset	17.3	9.9	45 - 55	F = 41.156, 5365.52 & 180.61 for higher concs at midnight for *C. capensis*, Sparidae Sp6 and *S. sagax* respectively. F = 32.176 for higher conc. at sunset for Gobiidae Sp1. F = 37.13 for higher conc. of all eggs excluding *E. japonicus* at midnight. F = 11.809 for larger E. whiteheadi larvae at sunset, and F = 41.05 for larger E. japonicus larvae at midnight.
								Midnight	18.3	10.2	25 - 40	
25-26/04/96	2179.2	252	23	489		7	25/04/96	Sunrise	15.6	10	8 - 20	H = 8.012 for larger P. costatus at midnight compared to day, H = 11.216 for larger M. capensis at sunset compared to day, H = 7.548 for larger Gobiidae Sp3 at midnight compared to sunrise, and H = 8.692 for larger A. pectoralis at sunset compared to sunrise and midday. H = 45.713 for combined larval sizes for each period, with midnight > sunrise/day & sunset > day.
								Day	18.6	9.8	No thermocline	
								Sunset	16	9.8	No thermocline	
								Night	14.9	9.8	5 - 23	
							26/04/96	Sunrise	12.7	9.8	No thermocline	No significant differences between sizes or concentrations were detected between sample times on this second day.
								Sunset	15	9.9	No thermocline	
								Night	13.9	9.9	No thermocline	

Of the seven species captured in March 1994, four were only recorded from one time period. The codlet *Bregmaceros atlanticus*, hake *Merluccius capensis*, and blenny *Scartella emarginata* were only caught during the late night stations, while the second blenny species, *Parablennius pilicornis*, was only sampled at sunrise. The redeye *Etrumeus whiteheadi* was the only species present in the sunset samples. The low larval concentrations, their absence from one or more of the sample periods (see Appendix 1), and the general pattern of heterogeneous variance complicated the statistical analysis. The Kruskal-Wallis test for all species and total larvae revealed the only significant difference was between concentrations of *Coccotropsis gymnoderma* (Table 3.3), which had a greater presence at midday than late at night. Variance among the mean sizes and size ranges of larvae (Appendix 2) was highly heterogeneous and no significant difference could be detected between sample times. Conversely, variance was homogeneous when all sizes were combined for each period with a significant difference being noted for the smaller midday caught larvae (Table 3.3). No flexion larvae were caught during the midday sample (Appendix 2). With the exception of a few preflexion *E. whiteheadi* at sunrise all other larvae were flexion/postflexion individuals.

Only four of the 18 species from the August 1994 samples were represented both at midday and at night, and the majority of species were present in low concentrations (Appendix 3). Fifty percent of the *P. pilicornis* larvae sampled during daylight had entered the flexion stage of development, with the rest of the late stage larvae coming exclusively from the night samples (Appendix 4). Of these, *Sarpa salpa* and Gobiidae Species 3 were single representatives from tows so patterns for these two species were not clear. The rest of the flexion animals were either *E. whiteheadi* or *S. sagax*, with a minimum of 50% of the larvae caught being in advanced stages of development. Two of the species which were well represented, *E. whiteheadi* and *S. sagax*, were significantly more abundant at night (Table 3.3) although the heterogeneity of variance for the former species reflects its absence from the daytime samples and presence in all three night tows. An unequal distribution of variance was also calculated for larval totals which exhibited significantly higher concentrations at night (Table 3.3), although it is assumed that the overall dominance of *E. whiteheadi* and *S. sagax* largely contributed to this result. While no difference in size between sample times could be detected for those species found at midday and at night, the heterogeneity in variance for *S. sagax* as well as the large size range (Appendix 4) may have masked the true pattern of larger larvae being caught at night. A look at overall lengths for all

species combined did reveal a significant difference (Table 3.3), with larger larvae appearing to be more susceptible to the gear at night.

Although species richness in November 1994 was high with 22 being recorded (Table 3.3), half of these were restricted to catches from one time period only (Appendix 5). The only significant difference in concentrations between time periods was detected for *Paracallionymus costatus* (Table 3.3) which was present in all three tows at sunrise but absent from all others (Appendix 5). Mean size, size range and percentage flexion for the catch are presented in Appendix 6, but statistical analysis could only be performed on those present at more than one station. Of the eleven species which met this requirement the only detectable difference was for *E. japonicus* (Table 3.3) where the larvae caught at midday were significantly smaller than those caught at sunrise. With all species grouped there was a significant difference between all three groups with mean sizes at sunrise being the largest followed by midday and lastly sunset (Table 3.3). Amongst the more abundant species there is a definite pattern of higher percentages of late stage larvae during the sunrise and sunset samples.

Of the 37 species of fish larvae caught over the two day period in October 1995, 24 were restricted to one of the days only. A large proportion of these were also only found either at sunset or midnight on those days and in very low concentrations (Appendix 7). On day 1 the concentrations of *Scomber japonicus* larvae were the only ones to register a significant difference (Table 3.3), although with a variance measure of P = 0 due their absence from sunset samples, the value of this result is questionable. The only other notable difference was found amongst the *E. japonicus* egg data where sunset concentrations were significantly higher than the midnight ones (Table 3.3). On the second day, concentrations of *Chelidonichthys capensis* and Sparidae Species 6 were significantly higher at night (Table 3.3). However their absence during sunset samples (Appendix 7) and the heterogeneity in variance should be noted. In addition, species such as *Boopsoidea inornata* and Gobiidae Species 2 exhibited high values at night as well and yet were not found to be significant, probably as a result of the unequal variance. Of the species present during both times and exhibiting homogeneous variance levels, *S. sagax* and Gobiidae Species 1 had significantly higher concentrations at midnight and sunset respectively (Table 3.3). Catches of eggs other than those identified as belonging to *E. japonicus* were significantly more abundant in the samples from the midnight stations (Table 3.3).

Only those species which were present in sufficient numbers on both days are discussed in terms of the results of the 2-way ANOVA for combined stations and days. A significant difference between stations in the absence of interaction for Gobiidae Species 1 ($F_{1,8}$ 25.992; $P < 0.05$) indicates that sunset samples were consistently higher over the two day period. The eggs of *E. japonicus* were present in significantly higher concentrations at sunset over the two days ($F_{1,8}$ 18.488; $P < 0.05$) although interaction between the two days indicates no consistent trends between sample periods. The remaining eggs were caught in significantly higher numbers at midnight on both days ($F_{1,8}$ 30.484; $P < 0.05$) as indicated by the absence of interaction.

In order to perform comparative analyses on size data there had to be larvae present at more than one time frame and there had to be more than one individual at that time. Single specimens allowed no degrees of freedom for error and hence could not be analysed by the ANOVA tests applied to separate and combined days. The high incidence of single larvae precluded many of the species from any further analysis (Appendix 8). Only six of the 37 fish species from each day which made up the total catch, and the squid para-larvae were subjected to size difference tests. On day 1, although all species exhibited greater sizes at midnight than sunset, only *S. sagax* and Gobiidae Species 2 showed significant differences (Table 3.3). The overall mean lengths followed the same trend with significantly larger larvae being ensnared during the late night samples (Table 3.3). Furthermore, all the larvae caught at sunset were preflexion fish, while a high percentage from midnight were in the flexion/postflexion stage of development. Mean sizes of squid para-larvae were practically the same although only a single animal was caught at midnight (Appendix 8). The pattern on day 2 was less defined, with late staged larvae coming from both sunset and midnight, depending on the species. The only significant differences were a larger mean size at sunset for *E. whiteheadi* and at midnight for *E. japonicus* (Table 3.3). The percentages of advanced staged larvae were more evenly distributed over the two time periods although some of the values for sunset samples were based on single individuals. Mean sizes of squid para-larvae were not significantly different, but were larger at midnight and comprised a larger size range (Appendix 8).

Variance in sizes tended to be heterogeneous for the time periods over both days but was mostly homogeneous between days. The 2-way ANOVA revealed that the mean size of *E. whiteheadi* was significantly larger at sunset on both days ($F_{1,8}$ 8.007; $P < 0.05$), while the reverse was evident for Gobiidae Species 2 with the midnight station producing the larger specimens ($F_{1,8}$ 13.978; $P < 0.05$). Larger *S. sagax* were dominant in midnight catches over both days ($F_{1,8}$ 13.499;

$P < 0.05$) as were those of *E. japonicus* (F, 37.974; $P < 0.05$) and *P. costatus* (F, 4.504; $P < 0.05$). With the exception of *E. whiteheadi* all other fish larvae had larger mean sizes from the midnight samples (Appendix 8). The same was true for all larvae combined and squid para-larvae although these were also not significant.

Appendix 9 contains the concentration data for individual species, larval totals, eggs and squid from the replicate tows over four time periods on April 25 and three on April 26 in 1996. On the first day, 19 of the 23 species were present during at least one time period as opposed to 17 on the second day. Nine of the species from day 1 were represented in only one of the samples periods compared with ten on the second day. Even amongst those species which displayed homogeneous variances there were no significant differences in concentrations between the four sample periods of day 1. At no stage when larvae were well represented did midday samples ever rank first, and in overall totals they came third after midnight and sunset samples. On the second day there were once again no significant differences between larvae, totals, eggs and squid although concentrations were mostly higher from the sunset and midnight samples (Appendix 9). The high incidence of larvae absent from tows together with overall low concentrations may explain why the Kruskal-Wallis test failed to detect differences over the two days.

When comparing both days combined, the midday samples from day 1 were excluded. The anchovy, *E. japonicus*, was present in significantly higher concentrations at sunset than at sunrise or midnight over the two day period (F, 10.018; $P < 0.05$) although the unequal variance ($P = 6.7$ E-4) reflected the absence of larvae from sunrise tows on both days and midnight samples on day 2. The result for Gobiidae Species 1 is more believable as variance for both sample time and day was homogeneous and the larvae were only absent from sunrise samples on day 2. There were higher concentrations at sunset, but only significantly so when compared to sunrise (F, 6.035; $P < 0.05$).

On April 25 1996 there were records of numerous flexion/postflexion larvae during the midday samples. However, the occurrence of these late stages were more frequent in the other samples, most notably at sunset and midnight (Appendix 10). The sunset samples on April 26 reflected the highest proportions overall of late developmental stages, with sunrise caught larvae comprising the lowest percentages. In all cases where sufficient larvae were present for comparison, sunset or midnight samples consistently produced larger specimens (Appendix 10). Overall, the ranking according to larval size was midnight followed by sunset and lastly sunrise. Significant differences

were detected on day 1 between midnight and midday for *P. costatus*, sunset and midday for *Merluccius capensis*, midnight and sunrise for Gobiidae Species 3, and sunset and sunrise/midday for *Austroglossus pectoralis* (Table 3.3). Overall totals for all larval sizes on day 1 showed a significant difference between midnight and sunrise/midday and between sunset and midday (Table 3.3).

Looking at both days combined, excluding midday on day 1, sunset and midnight samples produced the larger larvae for each species, totals and squid (Appendix 10). Gobiidae Species 3 showed a difference between midnight and sunrise (F, 5.28; $P < 0.05$), while *A. pectoralis* was also distinctly different between sunset and sunrise (F, 7.72; $P < 0.05$). The overall picture showed that sunset and midnight samples were similar, but both significantly different from sunrise catches (F, 9.7; $P < 0.05$).

Although catches in terms of concentrations and size were consistently greater in samples from periods of reduced visibility, significant differences were the exception and often only detected when numbers were low and variance high. The most obvious exceptions were the clupeiform larvae of *S. sagax* and *E. whiteheadi* which were mostly present in high concentrations and larger sizes, sometimes overwhelming the rest of the catch with this trend, as was the case in the midnight catches on 29/08/94. Certain species also featured more prominently in catches than others. *Sardinops sagax*, was present in significantly higher concentrations in night samples on two occasions, Gobiidae Species 1 was frequently most prominent, both in numbers and size, in sunset samples, and *E. japonicus* dominated sunset and midnight tows at times.

Perhaps one of the most important results was that on the occasions when two consecutive days could be sampled (October 1995 and April 1996), there were always differences between catches of individual species and overall species composition.

DISCUSSION

Zooplankters possessing well developed sensory systems (visual and neural) and swimming capabilities are able to perceive potentially harmful threats such as slow-hauled plankton nets and actively avoid them by means of a startle response (Blaxter & Fuiman 1989) which can be activated anywhere between 20 and 500 ms after perception of the danger (Batty 1989). This type of behaviour is exhibited by fish larvae and euphausiids predominantly during the day and in surface

waters (Clutter & Anraku 1968). The evasion of nets is not a phenomenon which is peculiar to fish larvae only. Ships' noises and visual stimuli have also been recorded as reasons for eliciting avoidance behaviour of purse seines in shoaling species such as herring, *Clupea harengus*, mackerel, *Scomber scombrus* (Misund 1993). Pacific bluefin tuna, *Thunnus thynnus oerientalis* (Inoue 1959; Scott & Flittner 1972), yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis* (Inoue *op. cit.*).

Although there was only limited data for mesh size comparisons, for reasons of convenience it was decided to use the larger 505 μ size for the duration of the project. For the most part, the mean sizes and size ranges of species captured in the two mesh sizes were greater for the larger 505 μ size, and many of the smaller size class individuals were also effectively caught in these nets. After testing nets with mesh sizes between 800 μ and 300 μ, Ahlstrom (1954) reached a compromise with a mesh size around 550 μ which he considered capable of retaining most sizes of *Sardinops caerulea* larvae. Presumably the overall design and smooth flow through the net and into cod-end buckets precluded to a large extent the flushing or extrusion of smaller larvae through the mesh. The higher proportion of flexion/postflexion larvae in the 505 μ mesh samples was seen as significant in terms of identification, as larger specimens lend themselves better to techniques such as clearing and staining, and meristics. The exclusion of Gobiesocidae Species 1 and *L. richardsoni* from the smaller mesh nets was not seen as significant, as many gobiesocids had already been sampled in 505 μ nets in August 1993 (see Chapter 2), and mullet species were a rare occurrence during the course of this study. In addition, the open-area ratio calculated for 333 μ mesh nets was 6.01. This is considerably lower than the 9.11 value for 505 μ and as such chances of clogging leading to backflushing and loss of samples is increased, as is the filtration pressure across the mesh leading to extrusion. The effectiveness of the hand operated bilge pump in flushing clogged small mesh nets was deemed questionable and between sample contamination was seen as a real threat. Smaller mesh sizes also retain higher concentrations of other plankton and debris (Schnack 1974; Smith 1981; Snyder 1983) which complicates and lengthens the sorting process. As most of the sorting was performed by one person, time was seen as a real constraint, so reducing the proportion of smaller organisms by using larger mesh sizes reduced the time and effort of sorting.

The observed differences in catch composition when sampling was conducted in the same area over two consecutive days demonstrated that the larval species assemblage was in a constant state of flux. The different species were either actively moving to maintain themselves in a favourable environment or being passively swept by oceanic and climatic forces in and out of the sampling zone. For these reasons, studies which deal with abundance and mortality estimates of ichthyoplankton, the major factors affecting stock stability (Marcy & Dahlberg 1980), usually involve the marking of a larval patch with a drogue so that it can be followed and continually sampled over a period of days.

Differences in catch composition, both numerically and taxonomically, between samples taken during different light intensities are common, e.g. *S. sagax* and *Engraulis ringens* were caught in significantly higher concentrations at night off Peru (Sameoto 1982) when a BIONESS multiple net sampler was used. However, the bias is not always in favour of the night samples. While high speed samplers are often considered to enhance extrusion, this effect may be reduced if a compromise is reached between towing speed and size of target organism such that catches between time periods are similar, e.g. Hinckley, Bailey, Picquelle, Yoklavich & Stabeno (1993) did not detect significant differences in catch rates of larval walleye pollock (*Theragra chalcogramma*) between day and night when using a 1 m Tucker trawl, although there was a detectable difference between catch rates at different depths.

Some of the early pioneers were aware of the discrepancy in catches arising from sample times. Intensive sampling by Russell (1926, 1928) revealed that pilchard, herring and sprat larvae were numerically more prominent in night time samples, while Marshall, Nicholls & Orr (1937) discovered that day sampling could not provide adequate numbers of herring larvae and had to resort to a night sampling regime. The undersampling of larger larvae during the day leading to false abundance and mortality estimates was experienced by Sette (1943) for *Scomber scombrus*, while Ahlstrom (1954) discovered that as Pacific sardine larvae increased in size so the disparity in catches increased. Larvae between 9.26 and 10.25 mm, and 15.26 and 16.25 mm were respectively up to five and nine times more numerous in night tows. Analysis of eight years of data from the northeast coast of the United States (Morse 1989) for all species of larvae combined showed ratios of day:night and twilight:night which were consistently greater than 1, often significantly so, regardless of season and most depth strata.

On an individual basis, 11 of 36 taxa showed significant differences favouring night and twilight catches over daytime samples, with 17 species exhibiting the trend of increased day:night ratios with larval size. Only one species, *M. aeglefinus*, was caught in higher numbers in daylight samples over all size ranges. For the rest there were variations of day exceeding night at smaller lengths and *vice versa* at larger sizes, or similar catches for both periods irrespective of size (Morse *op. cit.*).

It is logical to assume that larvae capable of swimming fast stand a better chance of evading capture if the net is detected in time. Unlike the case in adult fish, general morphology, while imparting much about motility, does not necessarily imply too much about mobility and speed. For example, Theilacker & Dorsey (1980 in Morse 1989) found that long bodied larvae such as *Clupea harengus* were fast swimmers as were the short bodied carangids *Trachurus symmetricus* and *Scomber japonicus*, while other long bodied larvae such as *Sardina pilchardus* and *Engraulis mordax* were slow swimmers. The startle response or C-starts of fish larvae to visual stimuli (Batty 1989; Blaxter & Fuiman 1989) is quick (20-60 ms), a function of size (distance covered is measured in body lengths per second), and usually away from the threat so that avoidance is only possible if the move is perpendicular to the towing direction. This also implies that smaller bodied larvae that are well developed and capable of swimming fast, may not evade capture if the net opening is too large.

The results obtained here showed that there was no dominant time period with respect to egg catches. Egg distribution may be in densely concentrated patches or could be diluted if conditions are right for their wide dispersal. Differences in egg catches would not have anything to do with visibility. Instead eggs could be lost through extrusion and escapement or missed altogether due to differential buoyancy characteristics, if all sections of the water column are not sampled. A good example of this was the high concentrations of *E. japonicus* eggs caught during the October 1995 samples. Although anchovy eggs had been caught previously (August 1995 - see Chapter 5) they numbered only a few and subsequent to the October catch were never again encountered. In this case vast amounts had been concentrated within the sample area and were being contained there, facilitating good catches in most replicate samples, as well as in the RMT samples used for assessing vertical distribution patterns (see Chapter 6).

The overall impression was that the bongo array being used with 505 μ mesh nets together with the method of towing was more than adequate for obtaining a representative sample of the available ichthyoplankton assemblage. While a faster towing speed may have helped capture more larvae and larger individuals it was assumed that it may also have lead to increased avoidance, both passive and active, due to pressure waves and clogging and increased vibrations and mechanical noise. As pointed out by Munk (1988) much of the catching efficiency is dependent on the relationship between avoidance and extrusion, as one is enhanced when the effect of the other is reduced. For the general purposes of seasonal distribution, the bongos were considered to be capable of providing the desired answers. In addition, unlike single net sampling arrays, the twin bongo nets on a single frame are ideal for the collection of replicate samples (Snyder 1983), thereby reducing time at sea and costs. Spatial distributional patterns such as depth preferences of larvae would have to be sampled with additional gear. This was accomplished with the RMT net on board the R.S. *Africana* (see Chapter 6). While the majority of the smallest of larvae were undoubtedly lost and many late developmental stages missed, the size ranges of specimens caught were in most cases representative of the majority of developmental stages for those species. In certain cases yolk-sac larvae and individuals in advanced stages of flexion were ensnared in the same net. The efficient flow through the net and the retention of larvae in the cod-end buckets reduced the potential for loss of small larvae through the mesh by escapement or extrusion. In addition, the larger mesh size minimised the risks of excessive clogging, backflushing and extrusion due to small mesh and made for the most convenient and cost/time effective sampling method.

It is acknowledged that observed catches were probably affected by more than just extrusion, escapement and avoidance. The physical environment can change rapidly as was seen over the two day periods during voyages #131 and #135 of the R.S. *Africana* when the positioning of the thermocline varied so much with depth, and sea surface temperature varied both temporally and spatially, especially during the second cruise (Table 3.3). Temperature not only influences movements and hence escape responses but may also be the chief determinant in meso-scale larval distribution and growth patterns (Kendall *et al.* 1984). Reduced catches may not reflect reduced gear efficiency but instead the absence of larvae as a result of environmental change. Larval absence could also be attributed to patchiness which is

related to either food concentrations or predator avoidance tactics, and vertical migrations away from the towing path for the same reasons. Additional reasons for vertical distributional patterns such as ocean currents, light intensity, salinity, and water temperature are alluded to at a later stage (see Chapter 6). Nevertheless, the effects of vertical avoidance was addressed when the entire depth profile, to within five metres of the substrate, was sampled by double oblique tows during the R.S. *Africana* and R.S. *Algoa* research cruises.

CHAPTER 4 - DESCRIPTION OF EARLY LIFE HISTORY STAGES OF SPECIES COLLECTED FROM THE SOUTH-EAST COAST OF SOUTHERN AFRICA

INTRODUCTION

The classification of fishes has in the past been almost solely based on the characters and relationships exhibited by juveniles and adults (Cohen 1984; Powles & Markle 1984). Adult characters seldom develop before larval metamorphosis and so the identification of early life history stages has historically been retarded due in part to the lack of quality microscopes, preservative mediums, clearing and staining techniques, and more recently, small mesh plankton nets. Information linking early stages to juveniles was lacking until work on commercially important fish species near the start of the century prompted scientists to look further than before (Ahlstrom & Moser 1981). These days curators are more willing to accept ichthyoplankton samples (Cohen 1984) - the most useful type being those comprising illustrated developmental series which can aid in furthering fish systematics. Powles & Markle (*op. cit.*) mention three strategies which are commonly employed to identify larvae, namely rearing eggs and larvae from known parent stock, tracing the development of adult characters backwards through a size series of larvae, and using a combination of these two together with affirmation from another worker or expert in the field. Further methods which may be used not only for identification purposes but also to enhance illustrations include clearing and staining techniques (Potthoff 1984; Taylor & Van Dyke 1985), radiography (Tucker & Laroche 1984), histology (Govoni 1984), scanning electron microscopy (Boehlert 1984), and developmental osteology (Dunn 1984).

The taxonomy and systematics of fishes is not the only field of research which benefits from the accurate identification of early life history stages. According to numerous authors, the many problems confronting fisheries biologists can also be solved in part through ichthyoplankton work. A short list of some of the more critical problems which are highlighted include fish distribution, fishery dynamics and management (including biomass estimations and recruitment), reproduction and ontogeny, species interactions, aquaculture and stock enhancement through seeding, isolating subpopulations or discrete spawner stocks, their importance in the ecosystem as prey, predators and grazers, productivity, oceanography, and impact assessments of environmental disturbances from natural phenomena and human

activities (Hempel 1974; Marcy & Dahlberg 1980; Gallagher & Conner 1983; Snyder 1983; Lasker 1987; Duarte & Mendonça 1989; Kendall & Matarese 1994).

Due to the ever increasing inclusion of ichthyoplankton work into fisheries and management fields, it is disturbing that of the 20 423 fish species mentioned in Moser *et al.* (1984) only 4% of the eggs and 10% of the larvae of these fish are known through descriptions and illustrations (Richards 1985). Looking at groups of fishes, the perciforms (which include a large proportion of the neritic species assemblage) are amongst the most neglected, with commercially important species, mostly from the North Atlantic region, belonging to the clupeiforms, salmons, tunas, flatfish and cods being well represented in the literature (Richards *op. cit.*). When viewing geographical regions separately the picture does not appear so bleak with up to 82 and 70 percent of larvae and eggs respectively being known from the North East Atlantic (Kendall & Matarese 1994). The South East Atlantic features quite prominently with 59 and 20 percent of its larvae and eggs respectively, thanks largely to Brownell (1979) and Olivar & Fortuño (1991). Kendall & Matarese (*op. cit.*) point out a number of regions for which publications and guides are either lacking or very few, one of which is the South Western Indian Ocean incorporating the eastern seaboard of South Africa. The reasons for the disparity in knowledge between regions can be attributed to the history of fisheries, presence of researchers, taxonomic diversity, and scientific interest.

Generally speaking there is a higher percentage of larvae known from regions with a history of large fisheries, where initial works at the turn of the century focused on fundamental biological studies. As harvest levels increased, the amount of research followed suit although certain major fisheries-orientated countries such as Japan were slow to start, with surveys commencing from as late as 1938 (Kendall & Matarese 1994). Large scale ichthyoplankton studies, in regions which had enormous fisheries potential, under the auspices of organisations such as the International Council for the Exploration of the Sea (ICES), Dana, Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, Food and Agriculture Organisation (FAO) and the California Cooperative Oceanic Fisheries Investigations (CALCOFI) led to the description of commercially important northern hemisphere species and the early life history stages of most are now known (Kendall & Matarese *op. cit.*).

Although South Africa has a long history of commercial exploitation, works on ichthyoplankton initially revolved around basic identification and biology, with studies aimed specifically at commercially important species being neglected until the latter half of the century (see Chapter 1). These commercial species are important components in the inshore and offshore demersal and pelagic trawl fisheries (Armstrong & Thomas 1989; Crawford 1989; Payne 1989; Payne & Crawford 1989; Badenhorst & Smale 1991; Smale & Badenhorst 1991) as well as the linefishery (Hecht & Tilney 1989; Penney, Buxton, Garrat & Smale 1989). Studies on the ichthyoplankton of reef dwelling species such as sparids and serranids which are important components of the commercial and recreational linefishery (Penney *et al.* 1989) are, however, few and far between. Authors have described various stages of development for only 13 of the 41 sparid species which may be found in South African waters, namely *Argyrozona argyrozona*, *Chrysoblephus gibbiceps*, *Chrysoblephus laticeps*, *Cheimerius nufar*, *Rhabdosargus globiceps*, *Rhabdosargus sarba*, *Diplodus cervinus hottentotus*, *Diplodus sargus capensis*, *Gymnocrotaphus curvidens*, *Lithognathus mormyrus*, *Pachymetopon blochii*, *Spondyliosoma emarginatum*, and *Sarpa salpa* (see Gilchrist 1903, 1916; Ranzi 1933; Brownell 1979; Kinoshita 1986; Okiyama 1988; Beckley 1989; Davis & Buxton 1996; Davis 1996; Connell, Heemstra & Garratt 1998). Considering that most of our sparids are endemic and important components of the linefishery, this is a sorry state of affairs. The identities of more are known but have not yet been described in the literature and as such are not readily available as a reference. These additional sparids include *Crenidens crenidens*, *Rhabdosargus holubi*, *Rhabdosargus thorpei*, *Acanthopagrus berda*, and *Pagellus bellotti natalensis*. Work on another mainstay species in the recreational linefishery, the galjoen *Dichistius capensis* (see Bennett & Attwood 1993; Attwood & Bennett 1994), has centered around its behaviour in captivity and potential for mariculture (van der Lingen 1986, 1991, 1994) with a more recent description of larval development in the species and a revision of its phylogeny with respect to *Dichistius multifasciatus* and other closely related families (Leis & van der Lingen 1997).

The objective of this section of work was to illustrate and describe the early life history stages of those species which have not yet received attention in the literature. A total of 28 larval types are presented here, representing nearly 37.3% of the taxa identified during this

project (see Table 5.1 in Chapter 5). This high percentage is an indication of just how little is known about the ichthyoplankton assemblage from the neritic region along the south-east coast of South Africa. It was envisaged that these illustrations and descriptions would significantly contribute towards the taxonomic status of ichthyoplankton research in South Africa while acting as a further reference for future larval surveys in the region.

METHODS AND MATERIALS

Where possible, a representative size range of each species was removed from the main collection and stored separately in 70% ethanol. Those that were to be cleared and stained for morphological features were stored in 95% ethanol before being processed (Pothoff 1984). All larvae were drawn facing left with the aid of a *camera lucida* attached to a dissecting microscope. The exceptions to this were *Gymnammodytes capensis* and Gobiidae Species 4 which were damaged on their left sides and the sole *Austroglossus pectoralis*. Xanthophores were not illustrated, nor were structures such as myomeres if they were not clear. Vertebrae were counted where possible, but not illustrated. All terminology follows that of Leis & Rennis (1983) and Leis & Trnski (1989), whose works have been used as a template for the descriptive process. Larval measurements to the nearest 0.01 mm were performed using a dissecting microscope and an ocular micrometer. The following body measurements were made (after Leis & Rennis *op. cit.*):

BD - body depth, measured perpendicular to the base of the pectoral fin.

BL - body length, measured as notochord length in preflexion and flexion larvae and standard length in postflexion larvae.

ED - eye diameter, measured across the midline of the pigmented region of the eye.

HL - head length, measured from the tip of the snout to the posterior margin of the opercular membrane.

PAL - pre-anal length, measured from the tip of the snout along the midline to a vertical line through the posterior edge of the anus.

PDL - pre-dorsal fin length, measured from the tip of the snout along the midline to a vertical line through the origin of the dorsal fin or fin anlage.

SnL - snout length, measured from the tip of the snout to the posterior margin of the pigmented region of the eye.

All specimens used for these illustrations and descriptions have been accessioned into the collection at the J.L.B. Smith Institute of Ichthyology in Grahamstown, South Africa (RUSI numbers 57 400 - 57 444).

RESULTS AND DISCUSSION

Family - Myctophidae

Hygophum sp. (Figure 4.1)

Morphology - Only two preflexion larvae of similar size (3.7 mm BL) were caught. Body slender, with 33 (17 + 16) myomeres. Gut is uncoiled with multiple vertical striations and extends to 60% of the body length. No gas bladder was evident. The head is large (0.29 BL), and small teeth are visible in the lower jaw. The eyes are elliptical and stalked with a mass of choroid tissue at their base. No spination is present on the head. No fin anlagen, except the pectoral fin bud, are present and the finfold is still complete. No photophores were observed.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.59 - 0.64
PDL	0.33 - 0.35
HL	0.29 - 0.31
SnL	0.16 - 0.17
ED	0.08 - 0.11
BD	0.17 - 0.19

Pigment - There is no cranial pigmentation. The isthmus, cleithral symphysis and ventral fore-gut are lightly pigmented. Heavier melanophores are present along the lateral sides of the mid-gut and the dorsal surface of the hind-gut. A small amount of pigment is present on the finfold just posterior to the anus. Slanted bars of pigment are found on the ventro-lateral surface along the four myosepta immediately above the hind-gut and again starting at the fifth post-anal myomere and extending to the ninth.

Similar species - The paired pigment dashes along the isthmus and cleithral symphysis, the heavy peritoneal pigment on the dorsal hind-gut and the slanted pigment bars on the trunk and tail are all characteristic of the genus. In addition the low count of myomeres (33) sets this species apart from most other myctophid genera. The elliptical eyes with choroid tissue and striated gut are

found in other myctophids, but the extended gut in preflexion larvae sets it apart from similar species such as *Myctophum nitidulum*, *Symbolophorus boops*, *Scopelopsis multipunctatus* and *Diogenichthys atlanticus*. Some of the *Diaphus* species discussed by Olivar & Beckley (1995) have slender preflexion larvae like the *Hygophum* species, but they have round eyes and different pigment patterns. Similarly, this species differs from preflexion larvae of the most common myctophid found during the study, *Lampanyctodes hectoris*, which have less pigment and round eyes. Other myctophids such as some *Lampanyctus* and *Myctophum* species are short and deep bodied throughout development (Moser, Ahlstrom & Paxton 1984). The possession of elliptical eyes alone makes it very difficult to confuse this species with larvae from any other family found in southern African waters.

The adults of four *Hygophum* species, *H. hansemi*, *H. hygomii*, *H. proximum* and *H. reinhardtii*, have been reported in South African waters (Hulley 1986), with illustrations and descriptions of their larvae appearing in Olivar & Fortuno (1991). The larvae of two additional species, *H. bruuni* and *H. macrochir* have been collected off northern Namibia and are also presented by Olivar & Fortuno (op. cit.). The *Hygophum* species described in this work appears to represent a seventh species for Southern African waters.

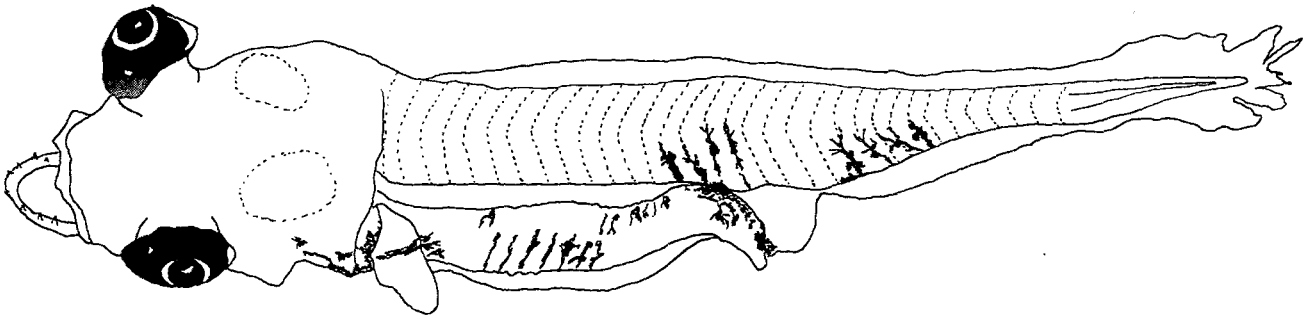


Figure 4.1 - Larva of an unidentified myctophid, *Hygophum* sp., from the south-east coast of South Africa. Stage - preflexion; BL - 3.71 mm; myomeres - 33 (17 + 16).

Family - Gobiesocidae

Gobiesocidae Species 1 (Figure 4.2)

Morphology - Description is based on 22 preflexion and flexion larvae ranging in size from 2.6 mm BL to 5.6 mm BL. Specimens encountered were typically torpedo-shaped and laterally compressed (Leis & Trnski 1989) in the preflexion stages, becoming more robust during flexion. Myomeres are often obscured by pigment (see below) but appeared to range from 23 (13 + 10) in preflexion specimens and 26-27 (15 + 11-12) in flexion animals. The number of vertebrae visible in a number of cleared flexion individuals was 27. All specimens above 4.3 mm BL were undergoing flexion. The gut is straight and slightly narrower in the early stages and extends beyond the midbody up to 68% of the body length. A prominent gas bladder is visible in most preflexion larvae, situated in the dorso-anterior section of the peritoneal cavity. This feature is not as prominent in flexion stages although heavy pigment may be responsible for obscuring its presence. The head is initially rounded, becoming more depressed in larger specimens. The mouth is large, but does not appear to extend to the anterior margin of the eye. Small, fine teeth are visible in the upper and lower jaws of flexion larvae. The eye is round. No head spination is present. While the pectoral fin buds are visible from early preflexion, no rays were visible, even amongst the largest larvae. The caudal fin anlage appears first, just after flexion at approximately 4.3 mm BL, followed by the dorsal and anal anlagen and lastly the pelvic fin bud. The full fin complements had not been attained in the largest specimen where the counts were D5, A5, V3, C19. The pelvic fin had not yet begun to transform into a suction disc.

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.65 - 0.67	0.67 - 0.68
PDL	0.17 - 0.21	0.13 - 0.25
HL	0.23 - 0.28	0.22 - 0.27
SnL	0.12 - 0.15	0.12 - 0.14
ED	0.07 - 0.11	0.08 - 0.09
BD	0.15 - 0.18	0.19 - 0.20

Pigment - Like most gobiesocids, pigmentation, especially over the trunk and tail is heavy. Melanophores are visible over the otic capsule and midbrain region in all larvae except the largest, with a few scattered stellar melanophores on the isthmus and cleithral symphysis in all larvae. In some flexion specimens there may be a small amount of pigment on the operculum and beneath the

angle of the lower jaw. In the smallest preflexion larvae, pigment is absent from the lateral and ventral portions of the mid- and hind-gut. The rest of the trunk and tail region, to approximately midway between the vent and tip of the notochord, is covered by discrete stellate melanophores. This pattern expands to include all regions of the gut in larger larvae. In the largest flexion larvae, pigmentation is still extensive but more diffuse over the entire trunk and tail region.

Gobiesocidae Species 2 (Figure 4.3)

Morphology - Description is based on 12 larvae ranging in size from 3.2 mm to 7.1 mm BL. Basic shape was similar to that of Gobiesocidae Species 1. Differences included a broader gut in preflexion larvae and a large mouth which extended past the anterior edge of the eye. The jaws appear to remain toothless. Myomeres ranged from 28 (13 + 15) in preflexion specimens and 31 (19 + 12) in flexion animals. Size at flexion is around 4.9 mm BL. Vertebrae were not visible even in large cleared specimens. A gas bladder was not visible beneath the heavy pigment on the trunk. Pectoral fin rays were not visible at any stage and the caudal fin anlage was again the first to appear, with a maximum of six rays being visible in the larger larvae. The pelvic fin bud was not yet discernible. Remnants of the fin fold were still present in the largest individual sampled (7.1 mm BL).

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.59 - 0.67	0.66 - 0.69
PDL	0.09 - 0.13	0.17 - 0.22
HL	0.22 - 0.25	0.19 - 0.28
SnL	0.12 - 0.14	0.13 - 0.17
ED	0.09 - 0.11	0.08 - 0.10
BD	0.17 - 0.21	0.18 - 0.20

Pigment - Pigmentation over the dorsal head region is heavy, either solid in preflexion larvae or as closely packed stellate melanophores in flexion larvae. Pigment along the angle of the lower jaw and on the margin of the pre-opercle becomes more pronounced in larger specimens, as do the melanophores on the isthmus and cleithral symphysis. Melanophores appear on the snout in flexion larvae, and diffuse stellate melanophores may be present beneath the lower jaw. The trunk and tail bear densely packed stellate melanophores which are interspersed with pigment bars following the

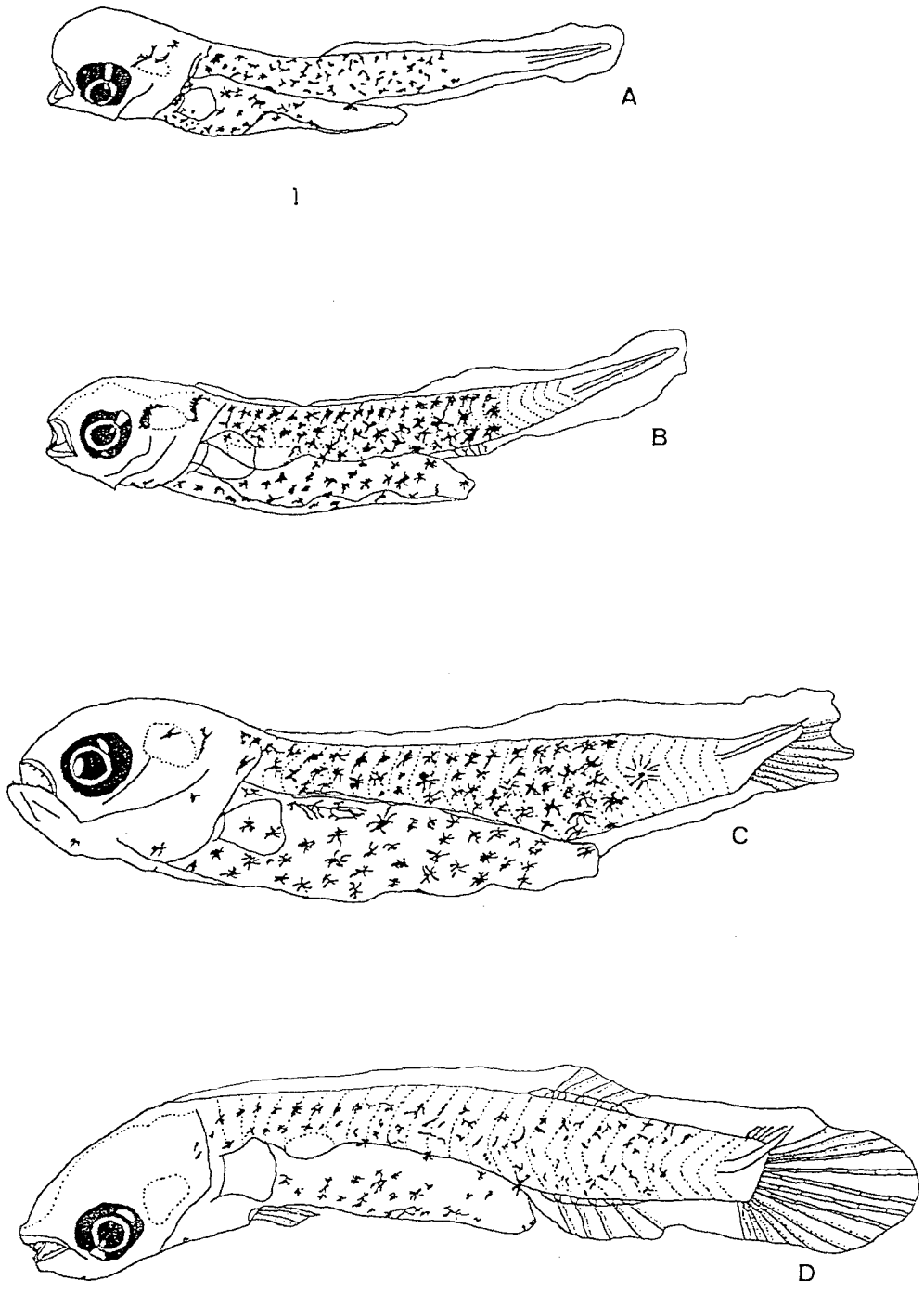


Figure 4.2 - Larvae of an unidentified gobiesocid, Species 1, from the south-east coast of South Africa. A: Stage - preflexion; BL - 2.82 mm; myomeres - not visible. B: Stage - preflexion; BL - 4.04; myomeres - 23 (13 + 10). C: Stage - flexion; BL - 4.22; myomeres - 27 (15 + 12). D: Stage - flexion; BL - 5.26; myomeres - 26 (15 + 11); 27 vertebrae.

contours of certain myosepta in preflexion animals. This heavy pigmentation ends abruptly after the fifth post-anal myomere. Areas devoid of pigment include much of the lateral head region, and two areas on the dorsal surface of the peritoneum in preflexion larvae and a single patch extending from the mid-lateral trunk region to just above the ventral gut and from the pectoral fin base to the anterior portion of the midgut in flexion larvae.

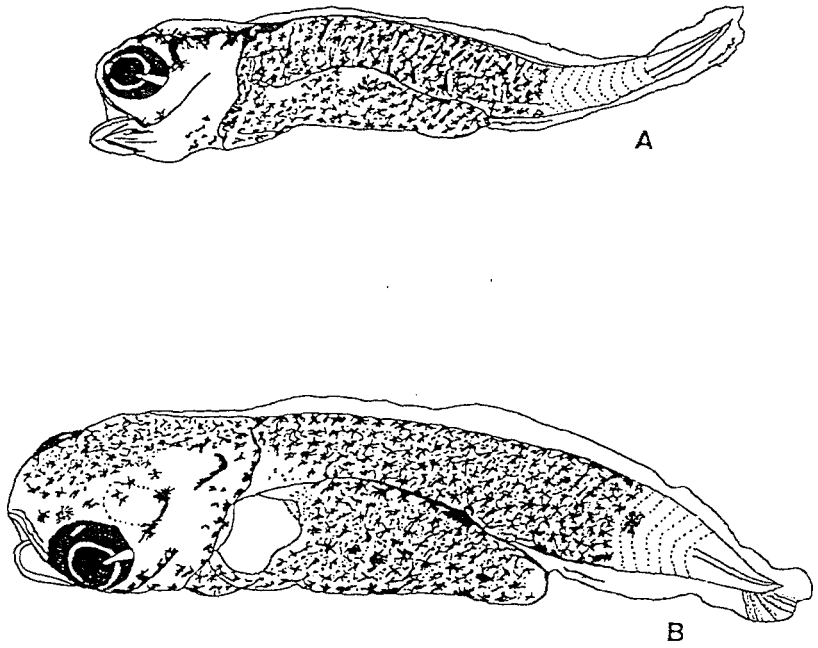


Figure 4.3 - Larvae of an unidentified gobiesocid, Species 2, from the south-east coast of South Africa. A: Stage - preflexion; BL - 3.4 mm; myomeres - 28 (13 + 15). B: Stage - flexion; BL - 5.11 mm; myomeres - 31 (19 + 12); 32 vertebrae.

Gobiesocidae Species 3 (Figure 4.4)

Morphology - Conforms to basic morphology of gobiesocid larvae. Description is based on five flexion larvae of similar size (4.58 - 4.63 mm BL). Gut is broad and extends up to 74% of BL. There are 28 myomeres (18 + 10). Mouth is large, extending past the anterior margin of the eye, and there are fine teeth in both upper and lower jaws. Sequence of fin development is not clear, but fin complements in the largest larva were D6, A5, P12, V3, C10. The anterior portion of the sucker

disc has begun to take shape, but is still in its infancy. Vertebrae were not discernible and neither was a gas bladder.

Morphometrics (as a proportion of body length):

	Flexion larvae
PAL	0.71 - 0.74
PDL	0.32 - 0.36
HL	0.28 - 0.31
SnL	0.16 - 0.17
ED	0.08 - 0.09
BD	0.19 - 0.22

Pigment - There are a few diffuse stellate melanophores over the mid-brain region, immediately above the dorsal margin of the pre-opercle and at the base of the pelvic and pectoral fins. A single melanophore is present at the cleithral symphysis. The dorsal peritoneal region bears the heaviest pigment, with a few scattered spots along the lateral peritoneum and four closely arranged melanophores on the ventral surface just anterior to the vent. A single melanophore is situated at the tip of the hind gut. Pigmentation on the trunk and tail is limited to a few diffuse spots starting at the ninth pre-anal myomere and ending at the 4th post-anal myomere. Four ventral stellate melanophores are situated close together immediately behind the vent.

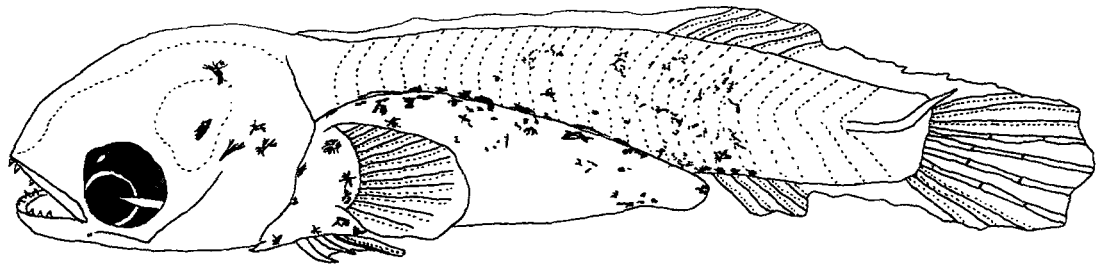


Figure 4.4 - Larva of an unidentified gobiesocid, Species 3, from the south-east coast of South Africa. Stage - flexion; BL - 4.61 mm; myomeres - 28 (18 + 10).

Similar species - According to Leis & Trnski (1989) gobiesocids are difficult to confuse with other species because of their long, uncoiled gut, heavy pigmentation, and sucker disc. The only similar family in terms of body form and pigment is the Exocoetidae, but elongate pectoral and pelvic fin rays and a caudal fin with its complete complement at hatching distinguish them from the clingfish.

Although the morphometrics of all three species are very similar, they are immediately distinguishable due to vastly different pigmentation patterns. Species 1 and 2 are both heavily pigmented, but Species 2 includes extensive covering on the head region and overall its melanophores are more densely arranged than in Species 1. Species 3 bears the least pigment and is the only one in which pectoral fin rays appear in flexion larvae. Species 2 also appears to have no teeth while the jaws of the other two exhibit numerous fine teeth. No postflexion specimens were caught, preventing positive species identifications based on sucker disc structure or fin complements. Adults of three species of clingfish, namely *Chorisochismus dentex*, *Apletodon pellegrini* and *Diplecogaster megalops* have previously been recorded from the study region and are most likely the same three species recorded here. A fourth species, *Eckloniaichthys scylliorhiniceps*, has only been recorded as far south as the Kei River on the east coast, but it is possible that the larvae of one species could also belong to this fish. Of these, only the yolk-sac larvae of *C. dentex* have previously been described (Gilchrist 1916), but the description is not sufficient to allow for any link to these species. The larvae of *Lecanogaster chrysea* described by Olivar (1987d) differ quite substantially with respect to pigment patterns, and has only been found off the Cunene River on the west coast of Africa.

Family - Haemulidae

Pomadasys olivaceum (Day, 1875 - Figure 4.5)

Morphology - Description has been based on flexion larvae, as the few preflexion specimens caught during the study were badly damaged during the clearing and staining process and were not included. Larvae are moderately elongate and laterally compressed. Myomeres numbered 26-27 (10 + 16-17), and 27 vertebrae were visible. The threshold size for the onset of flexion appeared to be 5.2 mm BL. The gut is coiled and extends to as much as 54% BL. The head is large, as is the mouth which extends well beyond the anterior margin of the round eye. Small, villiform teeth are present in the upper and lower jaw of all flexion larvae. Nares were distinguishable from the olfactory pit in larvae > 6.0 mm BL. A single supraocular spine appears in the smaller flexion larvae

with a second appearing in larvae > 5.5 mm BL. Both increase in size as the larvae grow. At 5.2 mm BL a supracleithral spine is evident, with a second one forming in larvae > 7.0 mm BL. Three pterotic spines were seen in the smaller flexion larvae. These decreased in size in larger larvae until only two were still visible in the largest specimens. Three spines are formed along the inner preopercle and five along the margin of the outer preopercle in all larvae. An array of spines appear for a short period on the opercle, cleithrum, angle of the lower jaw and immediately posterior to the margin of the eye at various stages during flexion. Dorsal, anal and caudal fin anlagen are all present during the early stages of flexion, with pectoral fin rays and the pelvic fin buds appearing in larvae > 7.0 mm BL. Dorsal and anal spines are present by 6.5 mm BL, and in the largest specimen the fin complement was DX,16; AIII,12; V4; P10; C17. A small gap is present between the vent and the first anal fin spine.

Morphometrics (as a proportion of body length):

	Flexion larvae
PAL	0.49 - 0.55
PDL	0.35 - 0.48
HL	0.28 - 0.31
SnL	0.17 - 0.18
ED	0.08 - 0.10
BD	0.21 - 0.26

Pigment - The angle of the lower jaw bears pigment in all stages, and a single stellate melanophore just anterior to the cleithral symphysis is present throughout. The tip of the lower jaw is lightly pigmented at first, becoming heavier in later stages. Pigment is present both ventrally and dorsally along the edge of the gut. This is initially fairly heavy but somewhat reduced in larger larvae. A large stellate melanophore marks the site for the base of the pelvic buds which appear only after 7.0 mm BL. The ventral edge of the tail initially bears melanophores at the base of the 4th, 6th and last post-anal myomeres. Slightly larger larvae have six large stellate melanophores at the base of the anal fin anlage with four smaller ventral spots towards the posterior section of the tail. Ventral tail pigment in the largest larvae has been reduced to two melanophores, one immediately behind the vent and another at the posterior edge of the anal fin. A single melanophore is present over the ventral caudal fin rays in the smaller larvae, while the larger specimens were seen to have two situated ventro-laterally at the base of the caudal fin.

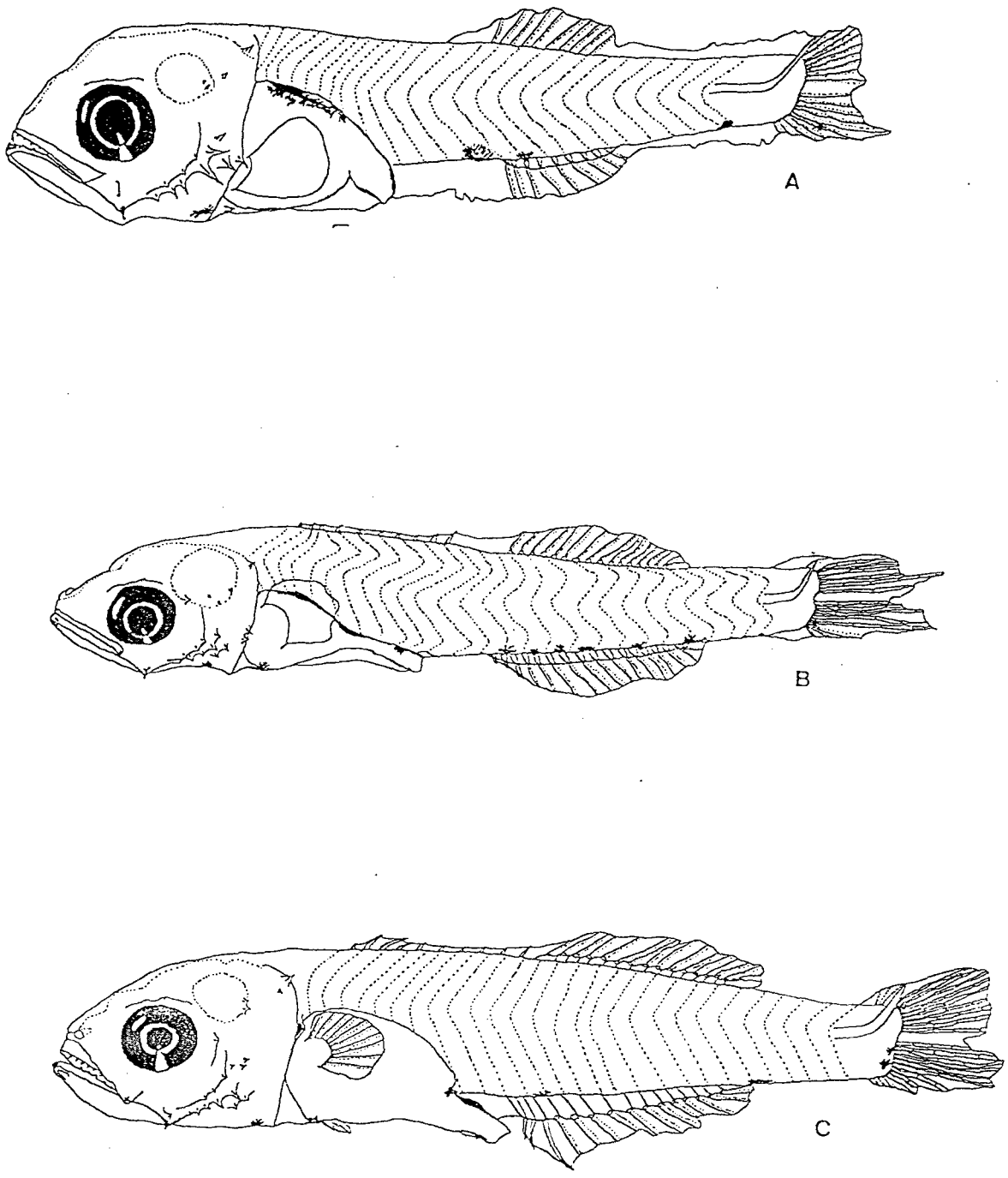


Figure 4.5 - Larvae of the haemulid, *Pomadasys olivaceum* (Day, 1875), from the south-east coast of South Africa. A: Stage - flexion; BL - 5.22 mm; myomeres - 26 (10 + 16); 27 vertebrae. B: Stage - flexion; BL - 6.72 mm; myomeres - 26 (10 + 16); 26 vertebrae. C: Stage - flexion; BL - 7.14 mm; myomeres - 27 (10 + 17). *Specimen B has been drawn from a moderately dehydrated specimen and hence the morphometric proportions do not coincide with those quoted for the species in the text.

Similar species - Haemulids, especially preflexion stages can be confused with larvae from a number of other families such as Lutjanidae, Serranidae, Nemipteridae, Sparidae, Gerreidae, Pomacentridae, Mullidae, Lethrinidae, Priacanthidae, Teraponidae, Opistognathidae and Sciaenidae (Leis & Trnski 1989) with respect to basic morphology, pigmentation and spination. However, differences in flexion and postflexion larvae are more distinct and close examination should set haemulid larvae apart from others based upon myomere counts, head spination pattern, pigment and fin counts (Leis & Trnski *op. cit.*).

Three species of haemulids have been found in the study area in the past, all belonging to the genus *Pomadasys*, namely *P. commersonnii*, *P. olivaceum* and *P. striatum*. A few recently metamorphosed *P. commersonnii* juveniles were examined but no clear resemblance could be found between them and the largest larva of 9.4 mm BL. *Pomadasys striatum* is rare in the study area, whereas *P. olivaceum* is abundant on subtidal reefs. The early life history stages of haemulids in southern Africa have been neglected by researchers, and prior to this study none had been described in the literature. As such any direct comparison with other haemulid larvae from the region was not possible. While fin development was not complete in the largest larvae collected here, spine and ray counts differ markedly between the three species (Smith & McKay 1986), and were closest to the complete counts of *P. olivaceum* which are DXII,15-17; AIII,11-13; P16-17.

Family - Sparidae

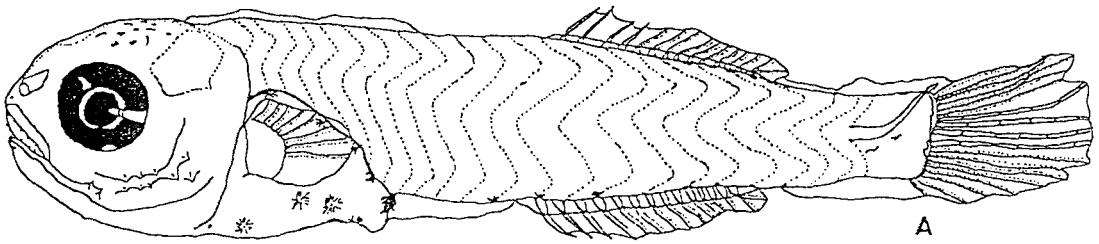
Boopsoidea inornata, Castelnau, 1861 (Figure 4.6)

Morphology (Table 4.1) - Description is based on flexion larvae only, as no preflexion specimens were sampled. Body depth moderate and laterally compressed with 23-24 (7-8 + 16) myomeres. Cleared specimens revealed 24 vertebrae. Gut is typically triangular and reaches between 41 and 45% BL. No gas bladder visible. Head moderately large with a gently rounded profile. Nostrils already appear separate from the olfactory pit in smallest larvae examined. Mouth reaches anterior margin of eye, extending as far as midpupil in larger larvae. Small, fine teeth are present in the upper and lower jaws. Eye is moderately large and round. All flexion larvae have three short, blunt inner preopercle spines and five larger, more robust spines on the outer preopercle. The smaller flexion larvae appear to have two spines close to the angle of the lower jaw and one on the sub-operculum just posterior to the largest spine on the outer preopercle. Dorsal, anal, pectoral and caudal fin anlagen are present by 5.5 mm BL with the pelvic fin buds appearing only in the larger >7.8 mm BL larvae. Dorsal and anal fin elements are ossified at 8.5 mm BL and

the complete fin complement at this stage matches that of the adult counts which are DXI.11; AIII.11; P15 (Smith & Smith 1986). In addition the pelvic fin count includes five rays and the caudal fin 20 (10 – 10) rays. A moderate gap exists between the vent and the origin of the anal fin.

Morphometrics (as a proportion of body length):

	Flexion larvae
PAL	0.41 - 0.45
PDL	0.22 - 0.38
HL	0.26 - 0.34
SnL	0.12 - 0.17
ED	0.10 - 0.13
BD	0.26 - 0.31



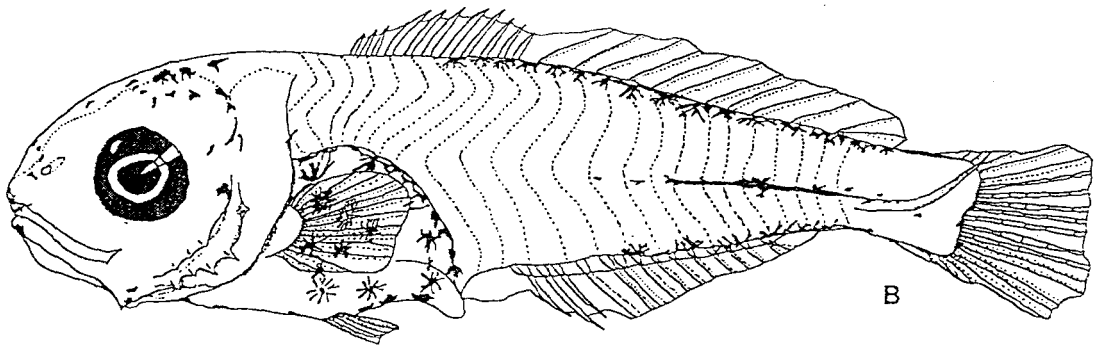


Figure 4.6 - Larvae of the sparid, *Boopsoidea inornata*, Castelnau, 1861, from the south-east coast of South Africa. A: Stage - flexion; BL - 6.81 mm; myomeres - 22 (7 + 15); 24 vertebrae. B: Stage - flexion; BL - 8.51 mm; myomeres - 24 (8 + 16); 24 vertebrae.

Pigment - In the smaller flexion larvae, two small pigment spots are visible on the tip of the snout and beneath the lower jaw, and a scattering of small stellar melanophores occurs over the fore- and mid-brain region with a larger one closer to the hindbrain. In larger larvae, the pigment in these regions becomes heavier and additional pigment appears at the angle of the lower jaw, at the dorsal edge of the inner preopercle and just posterior to the eye. The preopercle spines become lightly pigmented in large larvae as does the margin of the cleithrum. A single melanophore is present at the cleithral symphysis and the gut bears ventral, lateral and dorsal pigment which becomes heavier as the larvae approach postflexion. Dorsal and ventral pigmentation on the tail is light in small flexion specimens, but rapidly becomes heavier, expanding to include the caudal fin base and the mid-lateral posterior section over the notochord.

Sparidae Species 3 (Figure 4.7)

Morphology (Table 4.1) - Description is based on five preflexion larvae, as no flexion specimens were sampled. Body depth moderate and laterally compressed with 24-25 (6 + 18-19) myomeres. Vertebrae not yet visible. Gut is coiled and rounded, extending to 43% BL. Head moderately large with a rounded profile. Mouth extends back to midpupil level. No teeth visible in either jaw. Eye is moderately large and round. Preflexion larvae > 3.0 mm BL have three outer preopercle spines. No fin anlagen visible, except for pectoral fin bud, and finfold is complete.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.37 - 0.43
PDL	0.22 - 0.25
HL	0.24 - 0.26
SnL	0.13 - 0.15
ED	0.10 - 0.11
BD	0.22 - 0.24

Pigment - Head pigmentation is in the form of two large, faint melanophores over the forebrain and a single small spot near the hindbrain which disappears in larger preflexion larvae. The two melanophores over the forebrain become smaller but more distinct with size. In larvae > 3.1 mm BL, a single pigment patch appears in the region of the otic capsule and two spots are visible just posterior to the dorsal edge of the inner preopercle. Faint pigment which is visible along the ventral and ventro-lateral section of the gut in the smaller larvae becomes more visible in the form of four

Table 4.1 - Selected features used to identify the larvae captured in the study area between August 1993 and October 1996, which have been described and illustrated in this work. The abbreviations for head spination represent the following: IP - inner pre-opercle, OP - outer pre-opercle, LJ - angle of lower jaw, SO - sub-operculum, PT - pterotic, PRC - parietal crest, SPT - sub-pterotic, SC - supra-cleithral, SPO - supra-occular. Myomeres are presented as a total, followed by preanal + postanal components in parentheses.

Species	Stage	Myomeres	Vertebrae	GL(% BL)	Teeth	Mouth	Eye	Head Spination
MYCTOPHIDAE								
Hygophum sp.	Pre-flexion	33(17+16)	Not visible	60	Lower jaw only at 3.7 mm BL	Does not extend to anterior margin of eye	Elliptical and stalked with mass of choroid tissue	No spines
GOBIESOCIDAE								
Species 1	Pre-flexion	23(13+10)	Not visible	50 - 60	No teeth	Large, but does not extend to anterior margin of eye	Moderately large and round	No spines
	Flexion	26-27(15+11-12)	27	62 - 68	Upper and lower jaw	Large, but does not extend to anterior margin of eye	Moderately large and round	No spines
Species 2	Pre-flexion	28(13+15)	Not visible	50 - 60	No teeth	Large, extending past anterior margin of eye	Moderately large and round	No spines
	Flexion	31(19+12)	Not visible	65 - 69	No teeth	Large, extending past anterior margin of eye	Moderately large and round	No spines
Species 3	Flexion	28(18+10)	Not visible	65 - 74	Upper and Lower jaw	Large, extending past anterior margin of eye	Moderately large and round	No spines
HAEMULIDAE								
P. olivaceum	Flexion	26-27(10+16-17)	27	49 - 54	Upper and lower jaw	Large, extending past anterior margin of eye	Moderately large and round	3IP; 5OP; 2-3PT; 1-2SC; 1-2SPO
SPARIDAE								
B. inornata	Flexion	23-24(7-8+16)	24	41 - 45	Upper and lower jaw	Extends to anterior margin of eye or to midpupil	Moderately large and round	3IP; 5OP; 2LJ; 1SO
Species 3	Pre-flexion	24-25(6+18-19)	Not visible	37 - 43	No teeth	Extends to midpupil	Moderately large and round	3OP
Species 6	Flexion	24(8+16)	Not visible	44 - 47	Upper and lower jaw	Extends just beyond the anterior margin of the eye	Moderately large and round	2IP; 5OP; 1SO; 2PT; 1SC
Species 11	Pre-flexion	24(6-7+17-18)	Not visible	40 - 42	In both jaws at >4.0 mm BL	Extends just beyond the anterior margin of the eye	Large and round	2-3IP; 3-5OP; 1SO in < 4.0 mm BL; 2SPT
Species 10	Flexion	24(7+17)	Not visible	42 - 44	Upper and lower jaw	Extends just beyond the anterior margin of the eye	Large and round	1SPO; 3IP; 3OP

Table 4.1 continued.

SPARIDAE (cont.)								
Species 12	Pre-flexion	24(6+18)	Not visible	41	No teeth	Extends well beyond the anterior margin of the eye	Large and round	No spines
Species 13	Pre-flexion	25(11+14)	Not visible	61	No teeth	Extends just beyond the anterior margin of the eye	Moderately large and round	1IP; 3OP
SCIAENIDAE								
A. aequidens	Pre-flexion	26(11+15)	Not visible	51 - 53	Upper and lower jaw	Extends to midpupil	Moderately large and round	2OP; 2SPO
	Flexion	26(11+15)	Not visible	50 - 52	Upper and lower jaw	Extends to midpupil	Moderately large and round	4OP; 3SPO
Species 1	Pre-flexion	25(8+17)	Not visible	53	Upper and lower jaw	Extends to anterior margin of the eye	Moderately large and round	3IP; 3OP
	Flexion	25(8+17)	Not visible	47	Upper and lower jaw	Extends to midpupil	Moderately large and round	3IP; 4OP; 1SPT; 1SC
Species 2	Pre-flexion	25(9+16)	Not visible	50	Upper and lower jaw	Extends to midpupil	Moderately large and round	3IP; 3OP; 1SPO
CHEILODACTYLIDAE								
Species 1	Pre-flexion	34(15-16+18-19)	Not visible	53 - 68	No teeth	Moderatley large, extends to midpupil in smaller larvae	Moderately large and round	No spines
Species 2	Flexion	34(14+20)	Not visible	45 - 47	No teeth	Small, reaches anterior margin of eye	Moderately large and round	No spines
MUGILIDAE								
Species 3	Pre-flexion	21(11+10)	23	73	No teeth	Small, not reaching anterior margin of eye	Large and round	No spines
CHAMPSODONTIDAE								
C. capensis	Post-flexion	24(6+18) rest are partially obscured	Not visible	53	Upper and lower jaw	Large, reaching posterior margin of eye	Moderatley large and slightly elongate	5OP; 2PT; 3SC; 3PRC; multiple spines cover dorsal head surfaces
BLENNIIDAE								
Species 3	Pre-flexion	44(6+38)	Not visible	26	No teeth	Extends to midpupil	Large and round	No spines

Table 4.1 continued.

BLENNIIDAE (CONT.)								
Species 4	Pre-flexion	42(6+36)	39	25 - 28	Upper and lower jaw	Extends just beyond the anterior margin of the eye	Large and round	No spines
	Flexion (5.8 mm BL)	41(7+34)	39	27 - 29	Upper and lower jaw	Extends just beyond the anterior margin of the eye	Large and round	2IP; 7OP
Species 5	Pre-flexion	38(6-7+31-32)	Not visible	32 - 34	Upper and lower jaw	Extends just beyond the anterior margin of the eye	Moderately large and round	4OP
	Flexion (4.4 mm BL)	38(6-7+31-32)	Not visible	31 - 34	Upper and lower jaw	Extends just beyond the anterior margin of the eye	Moderately large and round	1IP; 6OP
Species 6	Pre-flexion	40(11+29)	Not visible	41	Upper jaw	Extends just beyond the anterior margin of the eye	Large and round	3IP; 2OP
	Flexion	41(8+33)	Not visible	28	Upper and lower jaw	Extends just beyond the anterior margin of the eye	Large and round	1IP; 2OP
AMMODYTIDAE								
G. capensis	Pre-flexion	Not distinct	Not visible	71	Upper jaw only	Small, extends to anterior margin of eye	Small and round	No spines
GOBIIDAE								
Species 1	Pre-flexion	25(9-10+15-16)	Not visible	51 - 56	No teeth	Extends just beyond the anterior margin of the eye	Moderately large and round	No spines
	Flexion (4.8 mm BL)	25(9-10+15-16)	Not visible	54 - 58	No teeth	Extends just beyond the anterior margin of the eye	Moderately large and round	No spines
Species 2	Pre-flexion	27(11-13+14-16)	Not visible	53 - 63	No teeth	Extends to midpupil	Moderately large and round	No spines
	Flexion (3.8 mm BL)	26(12+14)	Not visible	56 - 64	Upper and lower jaw	Extends to midpupil	Moderately large and round	No spines
Species 3	Pre-flexion	10 preanal, rest not distinct	Not visible	56 - 61	No teeth	Extends to anterior margin of the eye	Moderately large and round	No spines
	Flexion (4.0 mm BL)	24-26(9-11+13-15)	Not visible	55 - 66	In both jaws at > 5.0 mm BL	Extends to anterior margin of the eye	Moderately large and round	No spines
Species 4	Flexion	26(9+17)	Not visible	56	No teeth	Extends just beyond the anterior margin of the eye	Moderately large and round	No spines

Table 4.1 continued.

CYNOGLOSSIDAE								
C. capensis	Pre-flexion	46-57(6-9+37-50)	Not visible	33 - 37	In both jaws at 4.5 mm BL	Small, extending to posterior edge of pupil	Small and round	No spines
	Flexion	46-57(6-9+37-50)	Not visible	30 - 32	Upper and lower jaw	Small, extending to posterior edge of pupil	Small and round	No spines
SOLEIDAE								
A. pectoralis	Pre-flexion	8 preanal - rest not visible	Not visible	52	No teeth	Small, extending just past anterior margin of eye	Small and round	No spines
	Flexion	48-52(8+40-44)	Not visible	42	Upper and lower jaw	Large, reaching posterior margin of the eye	Small and round	No spines

large ventral stellar melanophores in larger specimens. Dorsal gut pigment is present and becomes heavier with size. Pigmentation along the ventral midline of the tail is continuous and heavy, with 11 distinct patches from just posterior to the vent to the notochord tip. In the larger preflexion larvae, there is a faint trace of pigment across the notochord immediately behind the last myoseptum

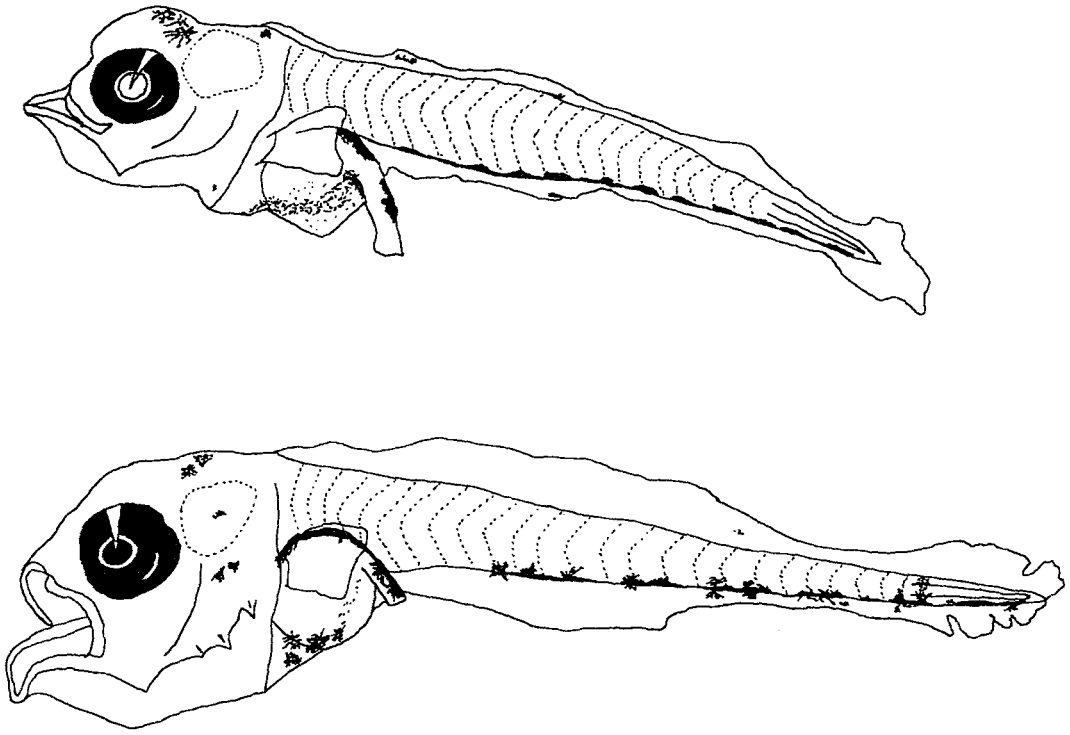


Figure 4.7 - Larvae of the unidentified sparid, Species 3, from the south-east coast of South Africa. A: Stage - preflexion; BL - 2.35 mm; myomeres - 24 (6 + 18). B: Stage - preflexion; BL - 3.13 mm; myomeres - 25 (6 + 19).

Sparidae Species 6 (Figure 4.8)

Morphology (Table 4.1) - Description is based on nine small flexion larvae between 4.31 and 4.71 mm BL. No preflexion specimens were sampled. Body depth moderate and laterally compressed with 24 (8 + 16) myomeres. Vertebrae not yet completely developed. Gut is coiled and triangular, extending to 47% BL. Head moderately large with a gently rounded profile. Mouth extends just beyond anterior margin of the eye. Small, fine teeth are visible in upper and lower jaw. Eye is moderately large and round. There are two short, blunt spines on the inner preopercle and five large, robust spines on the outer preopercle, with the largest being situated at the preopercular

angle. There is one subopercular spine immediately posterior to the preopercular angle, two pterotic spines and a single supracleithral spine. The pectoral fin bud is present, but no other fin anlagen are visible. The finfold is complete.

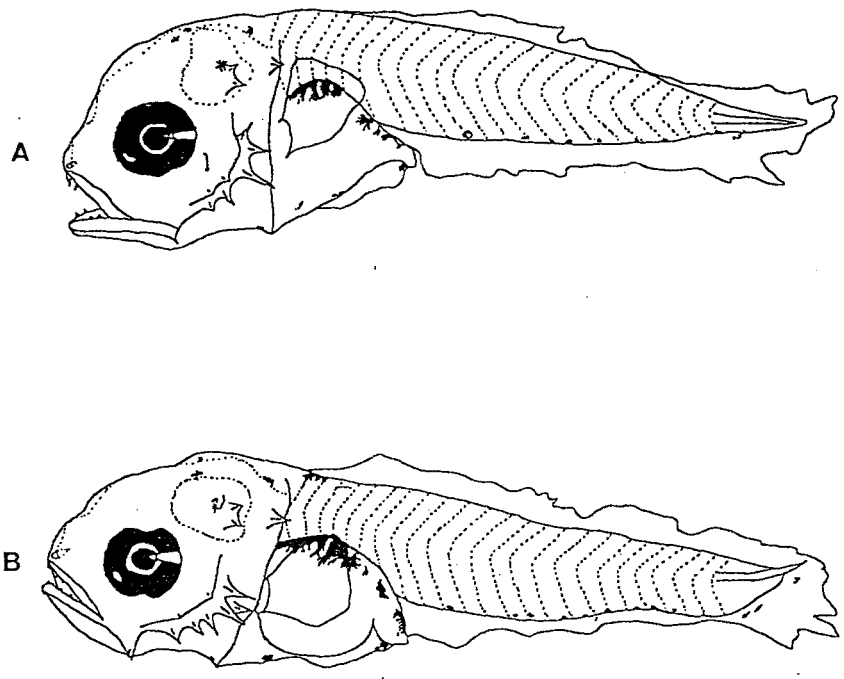


Figure 4.8 - Larvae of the unidentified sparid, Species 6, from the south-east coast of South Africa. A: Stage - flexion; BL - 4.31 mm; myomeres - 24 (7 + 17). B: Stage - flexion; BL - 4.71 mm; myomeres - 24 (8 + 16).

Morphometrics (as a proportion of body length):

	Flexion larvae
PAL	0.44 - 0.47
PDL	0.31 - 0.37
HL	0.26 - 0.29
SnL	0.16 - 0.17
ED	0.10 - 0.11
BD	0.29 - 0.39

Pigment - Small spots of pigment are present at the angle of the lower jaw and anterior to the cleithral symphysis. Two small stellar melanophores are situated over the midbrain, and single stellar melanophores are found over the otic capsule and hindbrain. A large melanophore is visible at the top of the first myomere along the dorsal midline. Ventral gut pigmentation is minimal, with a single melanophore along the ventral midline beneath the pelvic fin bud and one anterior to the vent on the finfold. Dorsal gut pigment is heavy, particularly over the fore- and mid-gut regions where it infringes slightly onto the lateral gut area. Ten small pigment spots are arranged along the ventral midline of the tail. A few scatterings of pigment appear on the most posterior part of the finfold.

Sparidae Species 11 (Figure 4.9)

Morphology (Table 4.1) - Description is based on 125 preflexion larvae between 2.25 and 4.12 mm BL. The few flexion specimens which were sampled were damaged during the clearing and staining process. Prior to this, however, it was determined that all larvae larger than 5.9 mm BL were in the flexion stage. Body depth moderate and laterally compressed with 24 (6-7 + 17-18) myomeres. Vertebrae not yet completely developed. Gut is coiled early and triangular in larger preflexion larvae, extending to 42% BL. Head moderately large, initially with a rounded profile which becomes more angled in larger specimens. Mouth extends just beyond anterior margin of the eye. Small, fine teeth are visible in upper and lower jaw in larvae > 4.0 mm BL. Eye is large and round. Head spines first appear at 3.2 mm BL. In the smaller larvae there are two short spines on the inner preopercle and three on the outer preopercle. There is also a single subopercular spine which is lost in larvae > 4.0 mm BL. The larger preflexion specimens have three short, blunt inner preopercle spines and five on the outer preopercle, the first three of which are short and blunt. The two at the preopercular angle are longer and more robust. Two small subpterotic spines immediately posterior to the eye are visible. The pectoral fin bud is present, but no other fin anlagen are visible. The finfold is complete.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.40 - 0.42
PDL	0.22 - 0.27
HL	0.25 - 0.29
SnL	0.14 - 0.19

ED 0.10 - 0.14

BD 0.22 - 0.31

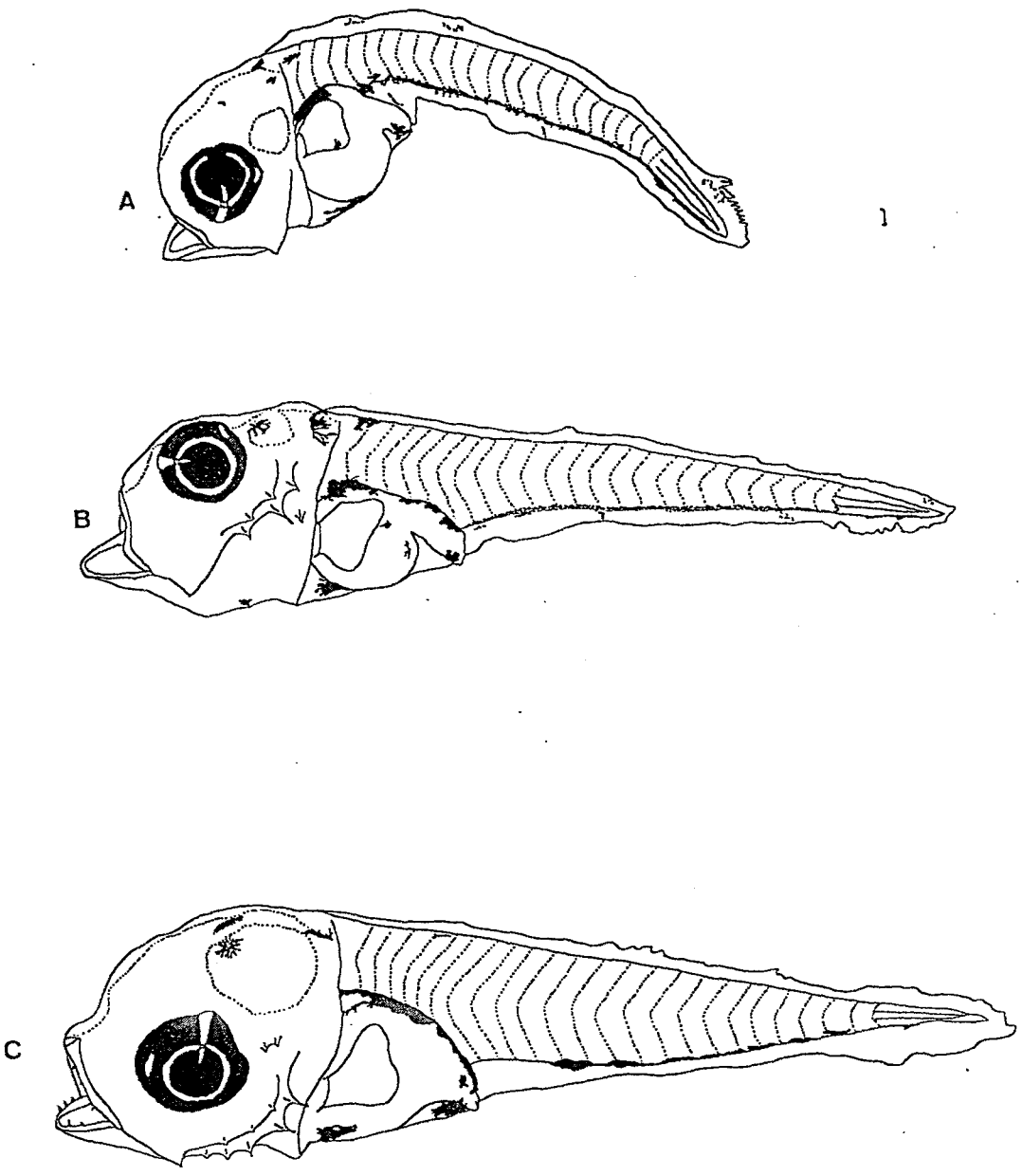


Figure 4.9 - Larvae of the unidentified sparid, Species 11, from the south-east coast of South Africa. A: Stage - preflexion; BL - 2.25 mm; myomeres - 24 (7 + 17). B: Stage - preflexion; BL - 3.41 mm; myomeres - 24 (6 + 18). C: Stage - preflexion; BL - 4.12 mm; myomeres 24 (6 + 18).

Pigment - The smallest preflexion larvae have a small pigment patch over the midbrain which is replaced by two large stellar melanophores in larger specimens. The hindbrain initially has two melanophores which form a single large stellar melanophore in larvae > 3.0 mm BL. A patch of pigment is also present at the dorsal origin of the first myoseptum, but this is lost in larger preflexion larvae. A single small melanophore may be present anterior to the cleithral symphysis along the ventral midline in some larvae. Dorsal gut pigment is first restricted to the anterior portion of the gut but quickly extends to cover the entire dorsal portion of the peritoneum. Lateral gut pigment is minimal and is restricted to one or two small melanophores in larvae < 3.6 mm BL. A large distinctive stellar melanophore is present throughout preflexion along the ventral midline beneath the pectoral fin bud, as is another melanophore which covers the anterior edge of the vent and the finfold in front of the vent. The ventral midline of the tail is covered with closely packed pigment spots from behind the vent to the posterior edge of the final myomere in larvae < 4.0 mm BL. From the edge of the final myomere to the tip of the tail, the pigment along the ventral midline is heavy and continuous. In larger preflexion larvae, eight large pigment patches are arranged along the ventral midline of the tail, starting between the bases of the 4th and 5th postanal myomeres, with the final patch close to the tip of the notochord. The finfold in some larvae bear small patches of scattered pigment spots.

Sparidae Species 10 (Figure 4.10)

Morphology (Table 4.1) - Description is based on three flexion larvae between 4.75 and 4.82 mm BL. No preflexion specimens were sampled. Body depth moderate and laterally compressed with 24 (7 + 17) myomeres. Vertebrae not yet completely developed. Gut is coiled and triangular in shape extending to 44% BL. Head moderately large with a rounded profile. Mouth extends just beyond anterior margin of the eye. Small, villiform teeth are visible in upper and lower jaw. Eye is large and round. There is a single supraocular spine over the anterior portion of the eye, three small inner preopercle spines, and three large, robust outer preopercle spines. The nares appear to be differentiated from the olfactory pit. The pectoral fin bud is present, as are the anal and caudal fin anlagen with their first elements. Caudal fin has 8 + 7 incipient rays and the anal fin has 14 incipient rays. The finfold is still complete.

Morphometrics (as a proportion of body length):

	Flexion larvae
PAL	0.42 - 0.44

PDL	0.32 - 0.36
HL	0.25 - 0.27
SnL	0.14 - 0.15
ED	0.10 - 0.12
BD	0.26 - 0.27

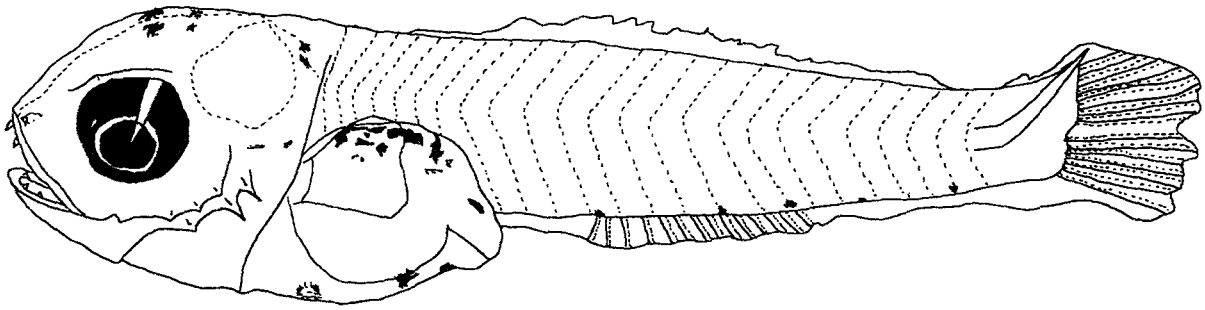


Figure 4.10 - Larva of the unidentified sparid, Species 10, from the south-east coast of South Africa. Stage - flexion; BL - 4.82 mm; myomeres - 24 (7 + 17).

Pigment - Two anterior and two posterior stellar melanophores are present over the midbrain, with two more behind the otic capsule over the hindbrain. Two small streaks of pigment mark the operculum just dorsal to the outer preopercle. The dorsal and dorso-ventral sections of the midgut are heavily pigmented, and a single melanophore is visible along the dorso-ventral surface of the hindgut. Three stellar melanophores are spaced along the ventral midline of the gut. Five small stellar melanophores are situated along the ventral midline of the tail at the base of the 4th, 8th, 10th, 12th and 16th myomeres.

Sparidae Species 12 (Figure 4.11)

Morphology (Table 4.1) - Description is based on two preflexion larvae, both 3.17 mm BL. No flexion specimens were sampled. Body depth moderate and laterally compressed with 24 (6 + 18) myomeres. Vertebrae not yet completely developed. Gut is coiled and triangular in shape extending to 41% BL. Head moderately large with a steeply rounded profile. Mouth extends well beyond anterior margin of the eye. Eye is large and round. The pectoral fin bud is present, but no other fin analgen are visible. The finfold is complete.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.41
PDL	0.16 - 0.26
HL	0.25 - 0.28
SnL	0.15
ED	0.10
BD	0.20 - 0.22

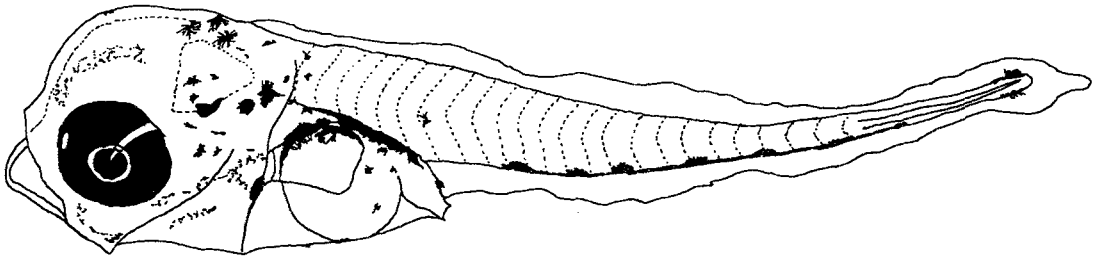


Figure 4.11 - Larva of the unidentified sparid, Species 12, from the south-east coast of South Africa. Stage - preflexion; BL - 3.17 mm; myomeres - 24 (6 + 18).

Pigment - The regions above the eye, around the angle of the lower jaw, preopercle and operculum have small pigment spots scattered over their surfaces. A collection of patches and stellar melanophores are distributed over the otic capsule, hindbrain and nape, supracleithral region and immediately posterior to the margin of the eye. Three larger stellar melanophores are visible over the midbrain. A large pigment spot is situated on the cleithrum at the ventral base of the pectoral fin bud. The dorsal fore- and mid-gut is heavily pigmented and a single small melanophore is found dorsally on the hindgut. A few small spots can be seen on the lateral portion of the midgut. There is a single medio-lateral melanophore at the 1st postanal myomere. Pigment along the ventral midline of the tail starts at the base of the 4th postanal myomere and is continuous to just past the last myoseptum. Amongst this pigment are six large melanophores at the base of the 4th, 7th, 9th,

12th, 15th and 17th myomeres. At the very tip of the notochord, there is a single melanophore on each of the dorsal and ventral edges.

Sparidae Species 13 (Figure 4.12)

Morphology - Description is based on a single 3.32 mm BL preflexion larva. Body depth moderate and laterally compressed with 25 (11 + 14) myomeres. Vertebrae not yet completely developed. Gut is coiled and triangular in shape extending to 61% BL. Head moderately large with a rounded profile. Mouth extends beyond anterior margin of the eye. Eye is moderately large and round. There is a single large inner preopercular spine and three large outer preopercular spines. The pectoral fin bud is present, but no other fin analgen are visible. The finfold is complete.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.61
PDL	0.23
HL	0.25
SnL	0.17
ED	0.09
BD	0.20

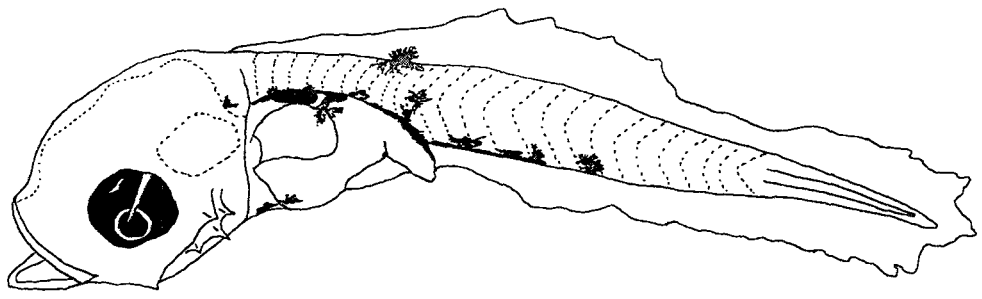


Figure 4.12 - Larva of the unidentified sparid, Species 13, from the south-east coast of South Africa. Stage - preflexion; BL - 3.32 mm; myomeres - 25 (11 + 14).

Pigment - A single small melanophore is visible on the hindbrain immediately posterior to the otic capsule. Ventral midline gut pigment is restricted to two melanophores beneath the pectoral fin base. Dorsal gut pigment is extensive and heaviest over the foregut region. A large stellar melanophore straddles the dorsal midline of the trunk from the 7th to the 10th preanal myomeres and extends onto the finfold. A medio-lateral melanophore is found on the 11th preanal myomere. Ventral midline tail pigment extends from behind the vent to the 7th postanal myomere and features four large melanophores at the bases of the 2nd, 4th, 5th and 7th postanal myomeres.

Similar species - Most of the characters used to describe sparid larvae which were found in the study area can also be applied to larvae from other percoid families such as the gerreids, teraponids, kuhliids, mullids, pomacentrids, nemipterids, sciaenids, plesiopids, ambassids and haemulids (Leis & Trnski 1989). However, none of these possess all the characters which define sparid larvae and can be discounted on the basis of a combination of gut size and shape, the gap between anal fin and vent, number of myomeres, ventral gut and tail pigment, general lack of cranial pigment in preflexion larvae, and preopercular spination.

South African sparid species whose larvae have previously been described include *A. argyrozona* (Davis & Buxton 1996), *C. nufar* (Connell, Heemstra & Garratt 1998), *C. laticeps* (Davis 1996), *D. c. hottentotus*, *D. s. capensis*, *L. mormyrus*, *P. blochii* (Brownell 1979), and *S. emarginatum* (Beckley 1989). A summary of the more readily identifiable features of the above larvae as well as *P. b. natalensis* are presented in Table 4.2. Although a flexion stage (6.9 mm BL) larva captured off Saudi Arabia was illustrated and briefly described by Houde, Altamar, Leak & Dowd (1986) as a "Type 3 sparid", details for Table 4.2 come from observations during this study and from Alan Connel of the CSIR. Larvae of all of these clearly differ from the species described in this study with respect to one or more of the following; number or ratio of myomeres, number or arrangement of head spines, size at flexion, size at which pelvic fin buds appear, and pigmentation (Table 4.2). Although larvae of *Sarpa salpa*, *Gymnocrotaphus curvidens* and several *Rhabdosargus* species have been described (Ranzi 1933; Melville-Smith 1978; Brownell *op. cit.*; Kinoshita 1986) they are limited to post-flexion and juvenile animals and are not suitable for comparison here. Okiyama (1988, page 532) described flexion and post-flexion stages of *Rhabdosargus sarba* from the Sea of Japan, but an untranslated text made comparisons awkward and an examination of the illustrations did not reveal any similarities with the larvae described here. Karrer (1984) has described and illustrated larvae of *Pagellus acarne* and *P. bogareveo* from the

Mediterranean sea which differ from *P. b. natalensis* in that they have no visible occipital crest. Furthermore, neither of these species bear any resemblance to those described in this work. A feature which can be used to identify postlarvae (> 10mm BL) of four Mediterranean species (*Boops boops, Oblada melanura, P. acarne* and *Sarpa salpa*) was also highlighted by Karrer (1984). These four species have unique anterior dorsal-fin supporting element arrangements. Once again similar features may prove useful amongst postlarvae of South African sparids, with *S. salpa* being found in our waters as well, but have no use here for comparison with smaller preflexion and flexion larvae.

Family - Sciaenidae

Sciaenidae Species 1 (Figure 4.13)

Morphology (Table 4.1) - Description is based on a single preflexion (3.21 mm BL) and a single flexion (5.52 mm BL) larva. Body depth moderate, with trunk and tail more compressed than head. There are 25 (8 + 17) myomeres. The gut is coiled and triangular, extending to 53% BL in the preflexion larva and 47% BL in the flexion larva. The head is large, with a gently rounded profile. The mouth is large and extends to the anterior margin of the eye in the preflexion larva and to the pupil in the flexion specimen. A few small teeth are visible in both jaws at an early stage but increase in number in the flexion larva. The nares appear to be differentiated from the olfactory pit in the flexion larva. The eye is round and moderately large. The inner preopercle bears three spines in both stages, while the outer preopercle has three in the preflexion stage and four in the flexion stage. In addition the flexion larva bears a subpterotic spine and a single supracleithral spine. The pectoral fin bud is present in the preflexion larva already while the caudal fin anlage with 6 + 6 incipient rays is present in the flexion specimen.

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.53	0.47
PDL	0.44	0.42
HL	0.37	0.32
SnL	0.21	0.20
ED	0.09	0.09
BD	0.32	0.33

Table 4.2 - Selected features from sparid larvae which have previously been described and illustrated, which can be used to distinguish them from those sparid species described in this work. The abbreviations for head spination represent the following: IP - inner pre-opercle, OP - outer pre-opercle, O - opercular, SO - sub-opercular, PT - pterotic, PTM - posttemporal, SPT - sub-pterotic, SC - supra-cleithral. The letters PV stand for Pelvic Fin, and the sizes indicate when the pelvic fin bud first appears. Myomeres are presented as a total, followed by preanal + postanal components in parentheses.

Species	Stage	Myomeres	Spines & PV	Pigmentation	Reference
A. argyrozona	Pre-flexion	25(7-9+16-18)	2OP	No head pigment. Dorsal gut surface is heavily covered, but ventral mid-line of gut and the cleithral symphysis are sparsely covered. A small pigment spot is present at the ventral midline base of each tail myomere.	Davis & Buxton 1996
	Flexion > 4.0 mm BL	25(10+15)	2IP; 7OP; 2SO, 1O, 2-3PTM; 3-5SC 7.58 mm BL	Extensive dorsally on head and snout tip and initially at lower jaw angle. Dorsal surface of hindgut initially, later stages bear little gut pigment. Most lateral areas of trunk and tail, and tail are extensively covered.	
C. nufar	Pre-flexion	24(9-10+14-15)	2-3OP	Otic capsule, snout and hindbrain surfaces show moderate coverage, with some pigment on the dorsal and dorso-lateral peritoneal surface.	Connell *et al.* in press
	Flexion	24(10+14)	3IP; 9-10OP; 1-2O, 1PTM; 2-5SC	Scattered over the head and nape region, and fairly extensive on dorsal peritoneal surface. Other than ventral midline pigment the tail bears no markings.	
C. laticeps	Pre-flexion	23-24(7-8+16)	1IP; 1OP	Sub-dermal pigment lines the otic capsule. Moderate levels of pigment are present on the dorsal surface of gut. Large melanophores mark the cleithral symphysis and ventral midline found along the ventral midline of the tail.	Davis 1996
	Flexion 4.95 mm BL	24(12+12)	5IP; 7OP; 2SO, 1O, 3SC 5.5 mm BL.	Cranial region covered by large melanophores, extending onto the nape and otic capsule region. Ventral midline and dorsal surface of gut are moderately covered as is the ventral midline of the tail. A large melanophore marks the posterior base of the dorsal fin anlage, visible along the ventro-lateral base of the caudal fin.	
D. c. hottentotus	Pre-flexion	25(7+18)	None present	The otic capsule and region above the eye bear some pigment. The gut and cleithrum are extensively covered, as is the mid-lateral trunk area from the operculum up to the mid-gut region. Light pigment marks the ventral mid-line of the tail, with the larger pre-flexion larvae bearing a large melanophore over the medio-lateral surface of the last myoseptum.	Brownell 1979
	Flexion	24(10+14)	4IP; 5OP; 1SO 7.9 mm BL.	Apart from the snout and lower jaw, the head as well as the nape and anterior trunk and gut are heavily pigmented. Ventral tail pigment comprises a few spots on anal fin elements and four melanophores between the distal edge of the anal fin and the caudal fin. Caudal section of the vertebral column also bears small traces of pigment.	
D. s. capensis	Pre-flexion	26(8+18)	None present	Head pigment is restricted to traces over the otic capsule and hind-brain in larger larvae. The cleithral symphysis, ventral midline of the gut and the dorsal peritoneal surface all bear pigment. Numerous small melanophores at myomere bases mark the ventral midline of the tail, with a single stellar melanophore along the dorsal midline of the tail at the 10th post-anal myomere.	Brownell 1979

Table 4.2 continued.

Species	Stage	Myomeres	Spines & PV	Pigmentation	Reference
D. s. capensis	Flexion 8.0 mm BL	24(10+14)	2IP; 6OP; 1SO; 2SC. 8.3 mm BL.	A pair of large melanophores mark the tip of the snout. Mid- and hind-brain regions as well as the preopercular and opercular region, nape and trunk are extensively covered. Large melanophores are present along the ventral midline of the tail and the caudal fin base.	Brownell 1979
L. mormyrus	Pre-flexion	25(7-8+ 17-18)	None present	The snout, hind-brain and otic capsule regions all initially bear pigment, but pre-flexion larvae >2.9 mm BL have no head pigment. Dorsal and ventral gut pigment gets heavier with size. Most post-anal myomeres bear a melanophore along their ventral mid-line base.	Brownell 1979
	Flexion 7.0 mm BL	24(10+14)	1IP; 2OP. > 8.0 mm BL.	The snout, cranial and nape regions are moderately covered, as are the dorsal and ventral midline gut surfaces. Dorsal and ventral midline pigment on the tail is restricted to the base of the fin anlagen, and the ventro-lateral edge of the caudal fin base is covered. A line of A line of pigment runs along the dorso-lateral edge of the vertebral column on the tail.	
P. blochii	Pre-flexion	26(8+18)	None present	A single melanophore marks the hindbrain and otic capsule regions. Pigment is otherwise restricted to dorsal and ventral surfaces of the gut and to 6 melanophores scattered along the ventral midline of the tail.	Brownell 1979
	Flexion 9.6 mm BL	24(10+14)	3IP; 8OP; 1SO 9.6 mm BL.	Cranial and nape regions and area immediately posterior to eye are heavily pigmented, as are dorsal and lateral peritoneal surfaces. Large isolated melanophores mark the ventral midline of the tail and small pigment spots mark the ventro-lateral edge of the caudal fin.	
P. h. natalensis	Pre-flexion	24(10+14)	3-4IP; 3-5OP; 1-2SO	The mid-brain bears two small pigment spots, with an additional mark on the cleithral symphysis. Dorsal and ventral pigment on the gut is very limited, and 3-4 large patches are evenly spaced along the ventral midline of the tail.	This study & Alan Connell Pers. Comm
	Flexion 5.5 mm BL	24(8+16)	3-4IP; 3-9OP; 3SO. > 8.5 mm BL.	Fore- and mid-brain and otic capsule regions bear stellar melanophores. The dorsal and dorso-lateral peritoneal surfaces are extensively covered. The tail bears ventral midline pigment, and the ventro-lateral caudal fin edge is also covered.	
S. emarginatum	Pre-flexion	24(6+18)	None present	Head pigment is limited to a single stellar melanophore over the mid-brain area in pre-flexion larvae >3.0 mm BL. Smaller larvae have no head pigment. The dorsal, ventral and anterior gut surfaces all have moderate pigment. A number of small spots cover the ventral midline of the tail, and in larvae >4.5 mm BL medio-lateral tail pigment starts to appear.	Beckley 1989
	Flexion 6.0 mm BL	24(7+17)	3IP; 5OP Approx. 8.5 mm BL.	Single stellar melanophores are present at the lower jaw angle and over the midbrain area. Ventral gut pigment is limited but extensive dorsally. Medio-lateral tail pigment is heavy, and two large patches mark the posterior bases of the dorsal and anal fin anlagen.	

Pigment - Head pigmentation on the preflexion larva consists of four small melanophores over the midbrain, three over the hindbrain and one large patch at the dorsal edge of the outer preoperculum. In the flexion larva a small melanophore is situated just dorsal to the nostril with three large stellar melanophores on the snout and a single large one immediately above the eye. The midbrain, hindbrain and otic capsule bear an assortment of small and large stellar melanophores. A single trace of pigment is also present just anterior to the third preopercular spine in the flexion larva. Ventral midline gut pigmentation is slight at first but becomes extensive at the flexion stage. Pigment along the anterior, lateral and dorsal surfaces of the gut also become heavier with size. A few scattered melanophores are located on the trunk above the gut on the first five preanal myomeres in both larvae. Three small melanophores are visible near the bases of the 11th and 15th postanal myomeres and near the ventral tip of the notochord in the smaller larva. These three pigment spots are slightly larger at the flexion stage and are located at the bases of the 7th, 13th and 16th myomeres.

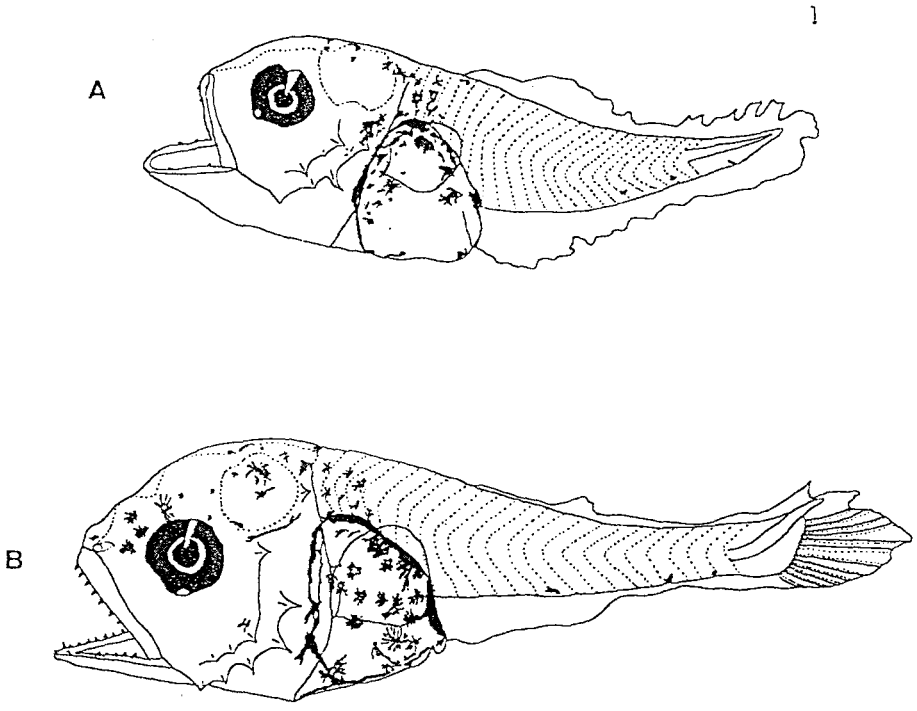


Figure 4.13 - Larvae of the unidentified sciaenid, Species 1, from the south-east coast of South Africa. A: Stage - preflexion; BL - 3.21; myomeres - 25 (8 + 17). B: Stage - flexion; BL - 5.52 mm; myomeres - 25 (8 + 17).

Sciaenidae Species 2 (Figure 4.14)

Morphology (Table 4.1) - Description is based on a single preflexion (3.27 mm BL) larva. Body depth moderate, with trunk and tail more compressed than head. There are 25 (9 + 16) myomeres. The gut is coiled and triangular, extending to 50% BL. The head is large, with a gently rounded profile. The mouth is large and extends to the midpupil. Numerous small teeth are visible in both jaws. The eye is round and moderately large. Three large, robust spines are present on each of the inner and outer preopercles, and there is a single short, blunt supraocular spine. The pectoral and pelvic fin buds are both present. The finfold is complete.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.50
PDL	0.34
HL	0.30
SnL	0.21
ED	0.12
BD	0.39

Pigment - The angle of the lower jaw is heavily pigmented, and single small patches of pigment are visible on the operculum and between the 2nd and 3rd outer preopercular spines. The ventral midline of the gut bears two stellar melanophores just anterior to the pelvic fin bud, which is covered in pigment itself. A large melanophore marks the pectoral fin base. Dorsal gut pigmentation is extensive, but heaviest over the hindgut section. Lateral gut pigmentation comprises medium to large stellar melanophores over the mid- and hind-gut surfaces. Four melanophores are located medio-laterally on the trunk, with two more near the dorsal origin of the first myomere. A single stellar melanophore is situated medio-laterally on the 8th myoseptum. A small melanophore is visible at the base of the 3rd postanal myomere, and a very large one covers the bases of the 6th - 9th postanal myomeres. A pigment patch can be seen on the finfold beneath the ventral edge of the 13th postanal myomere.

Similar species - Leis & Trnski (1989) state that sciaenid larvae may initially be confused with a few other percoid families, but can be separated on the basis of their short anal fin and exceptionally long dorsal fin. The robust body shape and large head also serve to distinguish some sciaenids, while the head spination patterns differentiate them from some co-occurring polynemid larvae. The three sciaenid species found in this study differ from each other with respect to the ration of preanal to postanal myomeres, head shape (profile) and spination, pigmentation, and size at which fin analgen appear.

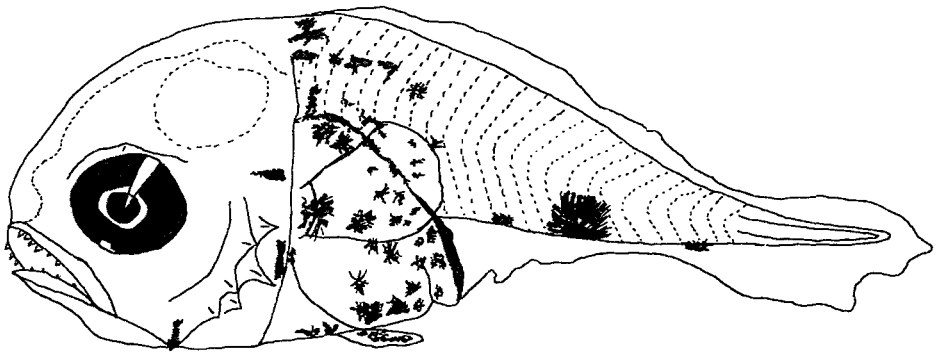


Figure 4.14 - Larva of the unidentified sciaenid, Species 2, from the south-east coast of South Africa. Stage - preflexion; BL - 3.27; myomeres - 25 (9 + 16).

The capture of four *A. aequidens* larvae during this study was surprising when considering the spawning behaviour of adult fish (Griffiths 1988). Identification was based on the single specimen previously caught in the area (Tilney & Buxton 1994) which had been tentatively identified (Jeff Leis, Australian Museum, Pers. Comm.). In addition, larvae of the closely related white seabass, *Atractoscion nobilis* (Moser, Ambrose, Busby, Butler, Sandknop, Sumida & Stevens 1983) closely resembled this species. Initial comparisons of the remaining two species with recently metamorphosed sciaenid juveniles from the area was of no help because of the size difference. Yolk-sac larvae of *Argyrosomus hololepidotus* measuring 3.3 mm SL sampled from the Swartkops Estuary (Melville-Smith 1978) were not similar, nor those between 2.2 and 24.8 mm BL described by Beckley (1990) which had poorly developed preopercular spines, a late developing pelvic fin bud (9.1 mm BL), and relatively little pigment. While no records of *Umbrina* spp. larvae were available it was initially thought that they were the most likely candidates. However, the recent

recognition that *A. hololepidotus* was a misnomer and that it actually comprised two species (Griffiths & Heemstra 1995) meant that what had previously been described as larval *A. hololepidotus* (see above) were in all likelihood the silver kob, *A. inodorus* (Griffiths 1996). So there remains another possibility that one of the unidentified species could be the offspring of the dusky kob, *A. japonicus*.

Family - Cheilodactylidae

Cheilodactylidae Species 1 (Figure 4.15)

Morphology - Description is based on 32 preflexion larvae between 2.09 and 4.75 mm BL. No flexion larvae were sampled during the study. Body is elongate and moderately compressed. There are 34 myomeres (15-16 + 18-19). The gut is straight and extends between 53% and 68% BL. The head is initially rounded but becomes more elongate in larger preflexion larvae, while the mouth is initially large, becoming relatively smaller with size reaching between the anterior margin of the eye and midpupil. The eye is round. No fin anlagen are present during preflexion, except for the pectoral fin bud, and the finfold is complete.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.53 - 0.68
PDL	0.20 - 0.24
HL	0.25 - 0.28
SnL	0.14 - 0.16
ED	0.09 - 0.11
BD	0.17 - 0.21

Pigment - Traces of pigment are present on the tip of the snout and the angle of the lower jaw in all larvae. Mid- and hind-brain pigment becomes more defined with size and a few melanophores appear just anterior to the cleithral symphysis in larvae > 4.0 mm BL. A narrow band of pigment extends along the midline from the posterior margin of the eye to the cleithrum. Pigment along the dorsal midline of the trunk and tail extends from the first myomere to the tip of the notochord and comprises between 13 and 17 stellar melanophores. Dorsal gut pigment is extensive over the entire surface and is continuous with the ventral midline tail pigment which extends to the edge of the final myoseptum. Variable amounts of pigment are always visible on the finfold in the region of the notochord tip. Ventral gut pigment extends from immediately behind the cleithrum to the vent and

comprises between twelve (smaller larvae) and eight (larger larvae) melanophores. Dorso- and ventro-lateral pigment is present from the final preanal myomere to the final postanal myomere in early preflexion larvae. It is lost in larger larvae to be replaced above 4.0 mm BL by small amounts of medio-lateral pigment.

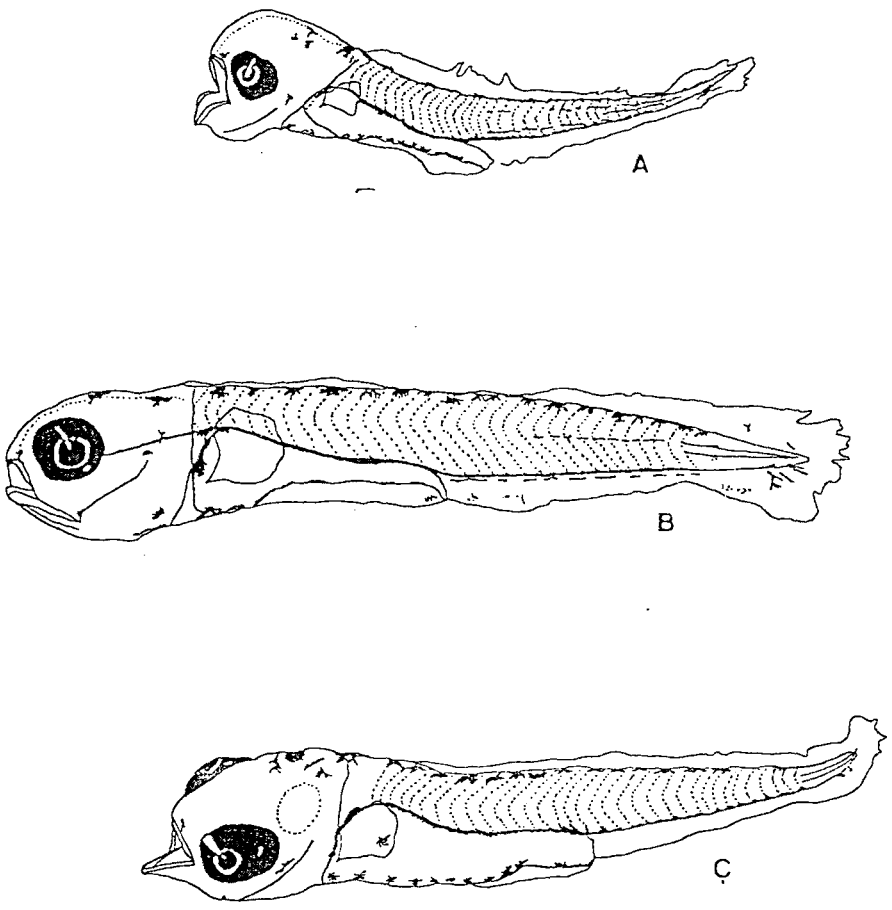


Figure 4.15 - Larvae of the unidentified cheilodactylid, Species 1, from the south-east coast of South Africa. A: Stage - preflexion; BL - 2.09 mm; myomeres - 34 (16 + 18). B: Stage - preflexion; BL - 3.80 mm; myomeres - 34 (16 +18). C: Stage - preflexion; BL - 4.31 mm; myomeres - 34 (15 + 19).

Cheilodactylidae Species 2 (Figure 4.16)

Morphology - Description is based on four flexion larvae between 5.12 and 5.35 mm BL. Body is elongate and moderately compressed. There are 34 myomeres (14 + 20) and stained specimens revealed 33 vertebrae. The gut is coiled along its anterior portion, but remains straight anteriorly.

extending up to 47% BL. The head is elongate with a small mouth which just reaches the anterior margin of the eye. The eye is round. The nostril appears to be differentiated from the olfactory pit. The pectoral fin bud is present but does not possess any differentiated rays. The caudal and anal fin analgen are visible with 5 – 7 and 6 incipient rays respectively. The finfold still appears complete.

Morphometrics (as a proportion of body length):

	Flexion larvae
PAL	0.47 - 0.51
PDL	0.34 - 0.37
HL	0.25 - 0.26
SnL	0.11 - 0.14
ED	0.09 - 0.10
BD	0.23 - 0.26

Pigment - There are small traces of pigment along the midline just anterior to the eye, over the midbrain, on the operculum, anterior to the cleithral symphysis, and on the pectoral fin membrane. While ventral gut pigment is extensive it comprises only small evenly spaced melanophores. Dorsal and lateral gut pigmentation is absent, and ventral midline tail pigment is limited to 11 small discrete spots starting at the 5th postanal myomere. Medio-lateral pigmentation is visible on the posterior half of the tail, and dorsal midline trunk and tail pigment is well developed, consisting of 17 - 18 large evenly spaced melanophores.

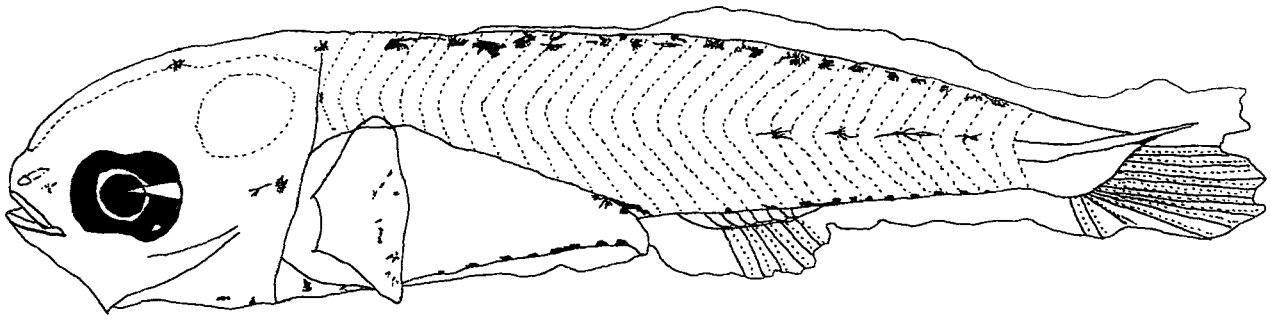


Figure 4.16 - Larva of the unidentified cheilodactylid, Species 2, from the south-east coast of South Africa. Stage - flexion; BL - 5.25 mm; myomeres - 34 (14 + 20); 33 vertebrae.

Similar species - Cheilodactylid larvae can be confused with coryphaenids and sillaginids in terms of general body shape and myomere numbers (Leis & Trnski 1989), but coryphaenids have head spination and heavier pigmentation while sillaginids have more ventral gut pigment and a more elongate head.

The only South African cheilodactylid species which has previously been described is *Cheilodactylus fasciatus* (Brownell 1979), although it was stated that there were no substantial grounds for it being chosen above *Chirodactylus brachdactylus*. Brownell's *C. fasciatus* differs from this Species 1 in several ways. It has 35-36 (17-18 + 17-18) myomeres, larvae appear to be poorly developed in the smaller preflexion size class, and while pigmentation is similar, it is not as extensive or heavy. Species 2 differs from Brownell's *C. fasciatus* and this Species 1 mainly in terms of its limited pigmentation and smaller mouth. It is acknowledged that Brownell's larvae were reared under controlled laboratory conditions and that these differences could be as a result of this, but until a larger size range can be described, no species can be attributed to these larvae as yet. There are, however, four possibilities, including *C. fasciatus*, as adult *C. brachydactylus*, *Cheilodactylus pixi* and *Chirodactylus grandis* are all found in the study area.

Family - Mugilidae

Mugilidae Species 3 (Figure 4.17)

Morphology - Description is based on a single 3.09 mm BL preflexion larva. Body depth moderate, and larva was robust and slightly compressed. There are 21 (11 + 10) myomeres, although heavy pigment may have obscured the true number. Twenty-three vertebrae were counted. The gut is slightly coiled but still elongate, extending to 71% BL. The head is large with a gently rounded, slightly concave profile. The mouth is small, falling short of the anterior margin of the eye. The eye is large and round. The caudal fin anlage is visible with its complement of six incipient rays. The finfold is complete.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.71
PDL	0.31
HL	0.32
SnL	0.19
ED	0.13

BD 0.30

Pigment - The tip of the snout and midbrain are heavily pigmented as is the immediate region around the cleithral symphysis and the midline between the posterior margin of the eye and the cleithrum. Smaller traces of pigment are visible over the fore- and hind-brain, the otic capsule and anterior to the eye. Six large melanophores mark the ventral midline of the gut, with the two nearest the vent being on the finfold. Dorsal gut pigment is minimal, but the lateral gut surfaces are covered extensively. Ventral midline tail pigment is restricted to four small groupings of melanophores, while dorsal midline tail pigment consists of densely packed small spots between the 1st and 8th postanal myomeres. The rest of the trunk and tail bears extensive lateral pigmentation ranging from large stellar melanophores to small patches to fine pigment spots as far back as the penultimate myomere.

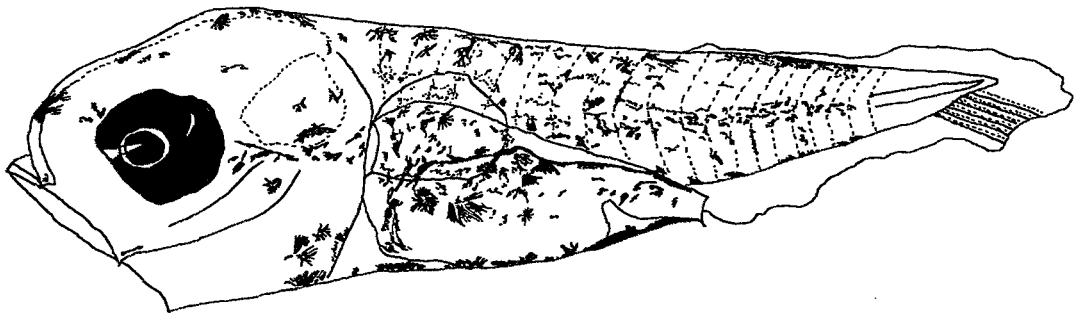


Figure 4.17 - Larva of the unidentified mugilid, Species 3, from the south-east coast of South Africa. Stage - preflexion; BL - 3.09 mm; myomeres - 21 (11 + 10); 23 vertebrae.

Similar species - There are not many other families with which preflexion mugilid larvae can be confused (Leis & Trnski 1989), although on occasion certain callionymids, toxotids and leptobramids may appear to be similar. Preflexion callionymids differ with respect to their robust gut and number of myomeres, and the toxotids attain flexion at a smaller size and posses head spination, while leptobramids have a different gut shape, and possess head spines and teeth.

The early life history stages of only two species of mullet from South Africa have been described, namely *Liza richardsonii* (Brownell 1979; Cambray & Bok 1989) and *Mugil cephalus* (Brownell *op. cit.*). Differences are not easily visible, although pigment is less extensive in *L.*

richardsonii and more extensive in *M. cephalus*, while the former has 22-23 myomeres and the latter has 24 myomeres. In addition, the caudal fin anlage and first few elements appear earlier in this species than either of the previously described species.

Family - Blenniidae

Blenniidae Species 3 (Figure 4.18)

Morphology (Table 4.1) - Description is based on three preflexion larvae between 3.65 and 3.98 mm BL. No flexion larvae were sampled during the study. Body is narrow and elongate, with a moderately compressed trunk and tail. There are 44 (6 + 38) myomeres. The gut is coiled and compact, reaching only 26% BL. The head is small and rounded with a large mouth reaching back to midpupil. The eye is large and round. There is no head spination, and apart from the pectoral fin bud no other fin anlagen are visible. The finfold is complete.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.23 - 0.26
PDL	0.12 - 017
HL	0.14 - 0.16
SnL	0.08 - 0.09
ED	0.08 - 0.09
BD	0.16 - 0.19

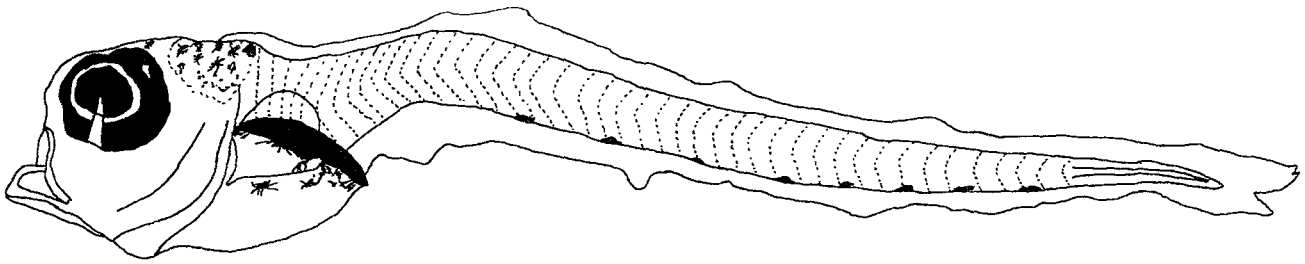


Figure 4.18 - Larva of the unidentified blenniid, Species 3, from the south-east coast of South Africa. Stage - preflexion; BL - 3.91 mm; myomeres - 44 (6 + 38).

Pigment - A couple of small melanophores are situated on either side of the midbrain, with nine to twelve stellar melanophores over the hindbrain and otic capsule surfaces. The dorsal and dorso-lateral surfaces of the gut are heavily pigmented, and sparse medio-lateral gut pigment is visible. Eight medium sized melanophores are located at regular intervals, starting at the base of the 11th postanal myomere along the ventral midline of the tail.

Blenniidae Species 4 (Figure 4.19)

Morphology (Table 4.1) - Description is based on preflexion and early flexion larvae between 3.62 and 6.92 mm BL. Body is narrow and elongate, with a moderately compressed trunk and tail. There are 42 (6 + 36) and 41 (7 + 34) myomeres in preflexion and flexion larvae respectively. Cleared specimens revealed 39 vertebrae. The smallest larva displayed no evidence of a yolk-sac, and flexion was evident in all larvae > 5.8 mm BL. The gut is coiled and compact, extending between 25% and 29% BL. The head is small with a gradually sloping, slightly concave profile at preflexion and a more convex appearance at flexion. The eye is large and round. The mouth is small and reaches just past the anterior margin of the eye. A few small, robust teeth are visible in the jaws of all larvae. Flexion larvae possess two small inner preopercular spines and seven outer preopercular spines. Only the pectoral fin bud is visible in preflexion larvae. The caudal fin anlage, with 5 + 7 incipient rays, appears in early flexion specimens. The finfold was complete in all larvae.

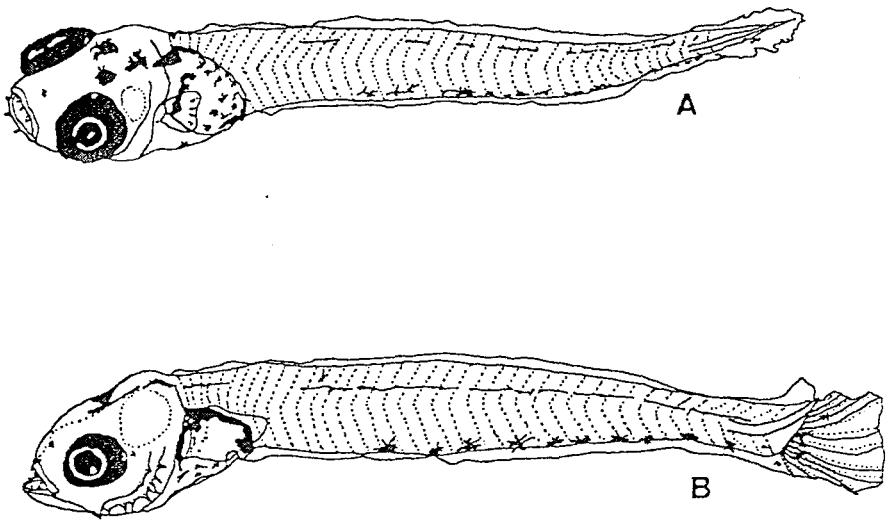


Figure 4.19 - Larvae of the unidentified blenniid, Species 4, from the south-east coast of South Africa. A: Stage - preflexion; BL - 5.81 mm; myomeres - 42 (6 + 36). B: Stage - flexion; BL - 6.91 mm; myomeres - 41 (7 + 34).

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.25 - 0.28	0.27 - 0.29
PDL	0.17 - 0.21	0.17 - 0.19
HL	0.17 - 0.18	0.17 - 0.19
SnL	0.14 - 0.15	0.11 - 0.13
ED	0.08 - 010	0.06 - 0.08
BD	0.16 - 0.17	0.15 - 0.17

Pigment - The most recognisable features are the three large stellar melanophores - two anteriorly over the midbrain and one posteriorly in the centre of the hindbrain. Traces of pigment also appear at the angle of the lower jaw and on the tip of the snout. The gut bears extensive pigment over the dorsal, lateral and anterior surfaces which becomes heavier in flexion larvae. The lateral gut stellar melanophores visible in smaller larvae are lost in larger animals. The ventral midline of the tail during preflexion bears a scattering of melanophores from the base of the 9th postanal myomere to the margin of the last myoseptum. This is replaced by 10 evenly spaced large melanophores starting at the 9th myomere and ending at the 30th postanal myomere in flexion larvae. A trace of pigment is visible on the finfold beneath the notochord tip in preflexion, while melanophores are distributed on the caudal fin membrane just posterior to its base in flexion larvae. A discontinuous line of dorso-lateral pigment stretches from the 5th to the 33rd postanal myomere initially, but is extended in larger larvae to include the 3rd postanal myomere and the first five preanal myomeres.

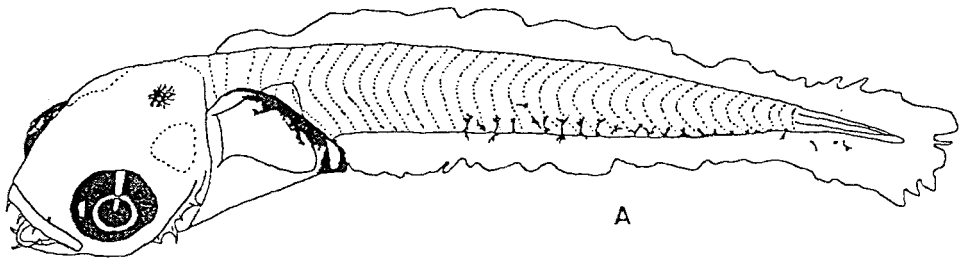
Blenniidae Species 5 (Figure 4.20)

Morphology (Table 4.1) - Description is based on preflexion and early flexion larvae between 3.48 and 4.53 mm BL. Body is narrow and elongate, with a moderately compressed trunk and tail. There are 38 (6-7 + 31-32) myomeres. The exact size at flexion could not be determined but is thought to be around 4.4 mm BL. The gut is coiled and compact, extending to 34% BL in both stages. The head is small with a gradually sloping convex profile. The eye is moderately large and round. The mouth is small and reaches just past the anterior margin of the eye. Preflexion larvae display a pair of moderately large canine teeth in the upper and lower jaws, which are replaced by numerous smaller villiform teeth after flexion. Head spination in the smaller larvae consists of four outer preopercular spines, while flexion specimens possess six outer preopercular spines and a

single spine on the inner preoperculum. Only the pectoral fin bud is visible in preflexion larvae, with the caudal fin anlage and 11 incipient caudal rays appearing in early flexion specimens. The finfold was complete in all larvae.

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.32 - 0.34	0.31 - 0.34
PDL	0.20 - 0.22	0.26 - 0.29
HL	0.19 - 0.20	0.26 - 0.28
SnL	0.14 - 0.15	0.14 - 0.16
ED	0.10 - 0.11	0.08 - 0.10
BD	0.16 - 0.18	0.20 - 0.23



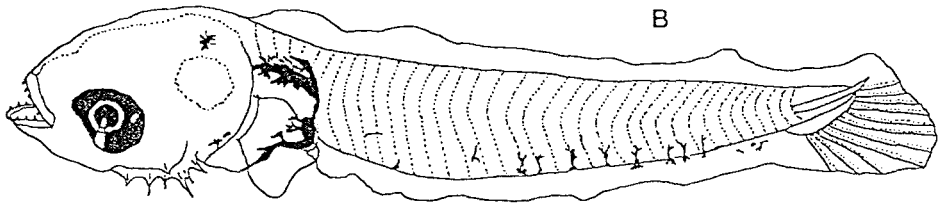


Figure 4.20 - Larvae of the unidentified blenniid, Species 5, from the south-east coast of South Africa. A: Stage - preflexion; BL - 3.57 mm; myomeres - 38 (7 + 31). B: Stage - flexion; BL - 4.52 mm; myomeres - 38 (6 + 32).

Pigment - A single large stellar melanophore is situated between the mid- and hind-brain in all larvae. Flexion larvae have additional head pigment in the shape of two small melanophores just

anterior to the cleithrum close to the dorsal edge of the outer preoperculum. In both stages, dorsal and dorso-lateral gut pigment is extensive and heavy, expanding to include much of the ventral gut and medio-lateral trunk surfaces. A mixture of stellar and Y-shaped melanophores are located along the ventral midline and ventro-lateral region of the tail from the 10th postanal myomere in all larvae. These melanophores overlap onto the finfold in places. This extends to the penultimate myoseptum in preflexion specimens and to the 25th in flexion larvae. Most larvae bear traces of pigment on the finfold towards the posterior section of the tail.

Blenniidae Species 6 (Figure 4.21)

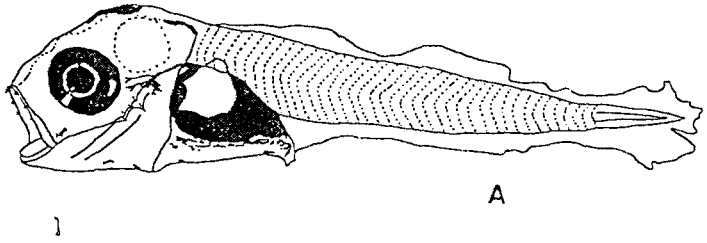
Morphology (Table 4.1) - Description is based on a single late preflexion (4.71 mm BL) larva and a single flexion (6.62 mm BL) larva. Body is narrow and elongate, with a moderately compressed trunk and tail. There are 40 (11 + 29) and 41 (8 + 33) myomeres in the preflexion and flexion specimens respectively. The gut is coiled and compact, extending to 41% and 28% BL in the preflexion and flexion larva respectively. The head is small with an irregular profile in the smaller specimen and a steeply rounded profile in the flexion larva. The eye is large and round. The mouth is small and reaches just past the anterior margin of the eye. Teeth were only visible in the upper jaw of the preflexion larva, but appeared in both jaws in the larger animal. Head spination in the smaller larva consists of two outer and three inner preopercular spines. The two outer spines persist in the flexion animal but only a single inner preopercular spine remains. The pectoral fin bud is present in the smaller specimen, but pectoral rays (12) only differentiate in the larger larva together with the first incipient caudal rays (4 + 5). The finfold is complete in both larvae.

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.41	0.28
PDL	0.25	0.31
HL	0.23	0.18
SnL	0.15	0.10
ED	0.11	0.08
BD	0.23	0.15

Pigment - Four to five large stellar melanophores cover the midbrain surface, with an additional one over the hindbrain in both larvae. The preflexion larva has additional traces of pigment at the angle of the lower jaw and on the isthmus, with a band of pigment along the midline from the eye

to the cleithrum. Ventral midline gut pigment is minimal in the small larva, but almost covers the surface in the larger specimen. Lateral and dorsal gut pigment is extensive and very heavy in both larvae, with the entire gut being covered at flexion. Trunk and tail pigment is absent in the preflexion larva. However, midline dorsal and ventral pigment is extensive on the tail of the larger larva in the form of closely arranged pigment spots. These range from the dorsal origin of the 1st and the ventral base of the 9th postanal myomeres to the posterior myoseptum of the 30th postanal myomere. A stellar melanophore is situated along the ventral midline just posterior to the last myoseptum and six narrow melanophores are spaced along the dorso-lateral surface of the tail between the 11th and the 30th postanal myomeres.



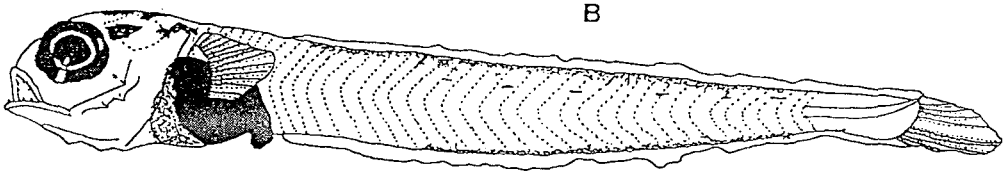


Figure 4.21 - Larvae of the unidentified blenniid, Species 6, from the south-east coast of South Africa. A: Stage - preflexion; BL - 4.71 mm; myomeres - 40 (11 + 29). B: Stage - flexion; BL - 6.62 mm; myomeres - 41 (8 + 33).

Similar species - Larvae from several other families may be mistaken at first for being blenniids. Included amongst these are certain myctophids, mugiloidids, triptervgiids, clinids, atherinids, and to a lesser extent some scombrids (Leis & Trnski 1989). However, none of these possess the entire suite of characters used to identify blenniid larvae and through a process of elimination can easily

be rejected. These characters include an elongate body, early coiling of the gut, preopercular spination, large canine teeth and long pectoral fin rays amongst certain blenniid tribes.

In southern Africa the larval stages of blennies have not received much attention, with four species, all found in the study area, having been described. Of these only *Parablennius pilicornis* and *Omobranchus woodi* have been described from recently hatched through to postflexion (Melville-Smith 1978; Olivar 1986). Two large (28 mm BL) postflexion *Parablennius cornutus* were described by Olivar & Fortuño (1991) and as such cannot be compared with the smaller larvae caught in this study, while only the preflexion stages of the fourth species, *Scartella emarginata*, have previously been dealt with (De Leo, Catalano & Parrinello 1976 in Olivar & Fortuño 1991). The four species described in this study, together with *P. pilicornis* and *S. emarginata* are all similar with respect to general body shape and morphometrics. However, they do show marked differences with respect to myomere numbers and ratios, head spination, size at flexion, size at which incipient pectoral and caudal fin rays appear, and in the extent of pigment covering and pigment patterns on the body and fins, in particular the pectoral fins and caudal fin base.

Family - Ammodytidae

Gymnammodytes capensis (Barnard 1927 - Figure 4.22)

Morphology - Description is based on a single (5.24 mm BL) preflexion larva. Body elongate and laterally compressed. Myomeres not distinct. Gut is long and uncoiled, extending to 71% BL. A small gas bladder is located over the foregut. The head is small with a rounded posterior and concave anterior profile. The mouth is small and just reaches the anterior margin of the eye. Numerous small teeth are visible in the upper jaw. The eye is small and round. The pectoral fin bud is present, and the caudal fin anlage with five incipient rays is visible. The finfold is still complete.

Morphometrics (as a proportion of body length):

	Preflexion larvae
PAL	0.71
PDL	0.30
HL	0.27
SnL	0.16
ED	0.05
BD	0.12

Pigment - A moderately large melanophore dominates the hindbrain, with a small trace of pigment at the tip of the snout, on the inner surface of the angle of the lower jaw and on the isthmus. A small melanophore is visible on the pectoral fin membrane with another near the ventral section of the fin base. The ventral midline of the gut and tail, and the dorsal midline of the gut possess series of small melanophores or pigment patches, with the tail pigment continuing almost to the anterior edge of the caudal fin anlage. The margin of the gas bladder is covered by small pigment markings.

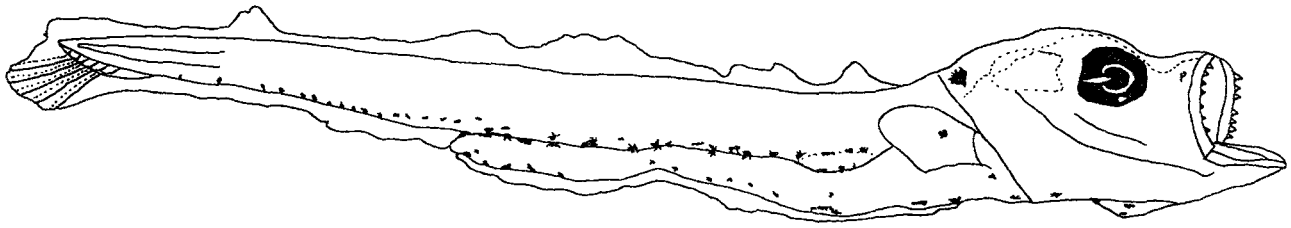


Figure 4.22 - Larva of the ammodytid, *Gymnammodytes capensis* (Barnard 1927), from the south-east coast of South Africa. Stage - preflexion; BL - 5.24; myomeres - not distinct.

Similar species - While a host of characters may be found to describe ammodytid larvae, they may be confused with other elongate larvae at first glance. However, preflexion clupeiform and gonorynchiform larvae display longer guts and less pigment, while microdesmids have a shorter gut and larger gas bladder (Leis & Trnski 1989). Early stage aulostomids are very similar except for a fractionally higher myomere count, and the lighter pigmentation and fewer myomeres distinguish schinleriids. Only two species of ammodytids are found in southern African waters. *Bleekeria remmiei* and *G. capensis*. The former is rare and found only as far south as East London on the east coast, while *G. capensis* is found around the entire coast of South Africa and is considered plentiful along the south coast.

Family - Gobiidae

Gobiidae Species 1 (Figure 4.23)

Morphology (Table 4.1) - Description is based on 18 preflexion and flexion larvae ranging in size from 1.7 to 5.81 mm BL. Larvae are elongate and round in cross section. There are 25 (9-10 + 15-16) myomeres. This species emerges at a small size because the larvae between 1.7 and 2.0 mm BL had yolk-sac remnants present. Larvae > 4.8 mm BL were considered to be in the flexion stage. The gut is uncoiled and slightly curved in smaller specimens, extending up to 58% BL. A gas bladder just forward of the midgut is visible in some larvae. The head is small with a gently sloping, slightly concave profile. The mouth is also small and just reaches past the anterior margin of the eye which is moderately large and round. The pectoral fin bud forms early on, but no elements had differentiated even in the largest specimens. Anal and caudal fin anlagen with five and eight incipient rays respectively have formed by 4.5 mm BL. By 5.75 mm BL the dorsal fin anlage has appeared with four incipient rays. At this stage the anal fin has one spine and five incipient rays, and the caudal fin has 6 + 4 fully formed primary rays and 3 + 2 incipient rays. The finfold is complete in larvae up to 4.72 mm BL, and absent by 5.0 mm BL.

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.51 - 0.56	0.54 - 0.58
PDL	0.26 - 0.35	0.29 - 0.72
HL	0.23 - 0.28	0.23 - 0.26
SnL	0.09 - 0.12	0.11 - 0.12
ED	0.06 - 0.07	0.07 - 0.09
BD	0.16 - 0.21	0.16 - 0.18

Pigment - Preflexion larvae bear no head pigment. Once flexion occurs, however, pigment appears beneath the posterior section of the lower jaw and at the angle of the lower jaw, with single large stellar melanophores visible at the cleithral symphysis and on the isthmus. The one on the cleithral symphysis is lost in larger larvae. The pectoral fin base is lightly pigmented at first and then moderately so by late flexion. Ventral gut pigment comprises seven large melanophores arranged along the midline between the cleithrum and vent. These first decrease in number to three or four in early flexion larvae before becoming more numerous, but smaller, in larger flexion specimens. There is heavy pigment over the dorsal surface of the gas bladder in all larvae and over the dorsal surface of the mid- and hind-gut in preflexion larvae. A broad band of pigment marks the

ventral midline of the tail from the vent to the edge of the final myoseptum in all larvae. Two large stellar melanophores also mark the base of the 7th and 9th postanal myomeres in larvae < 5 mm BL, while between six and seven are evenly spaced along the ventral midline in larger larvae. The caudal fin anlage bears a broad band of pigment in smaller flexion larvae, while the caudal fin base is covered with stellar melanophores in larger specimens. Closely arranged melanophores are situated along the dorsal midline of the tail between the 6th and 10th myomeres in preflexion larvae and 7th to 11th in flexion animals.

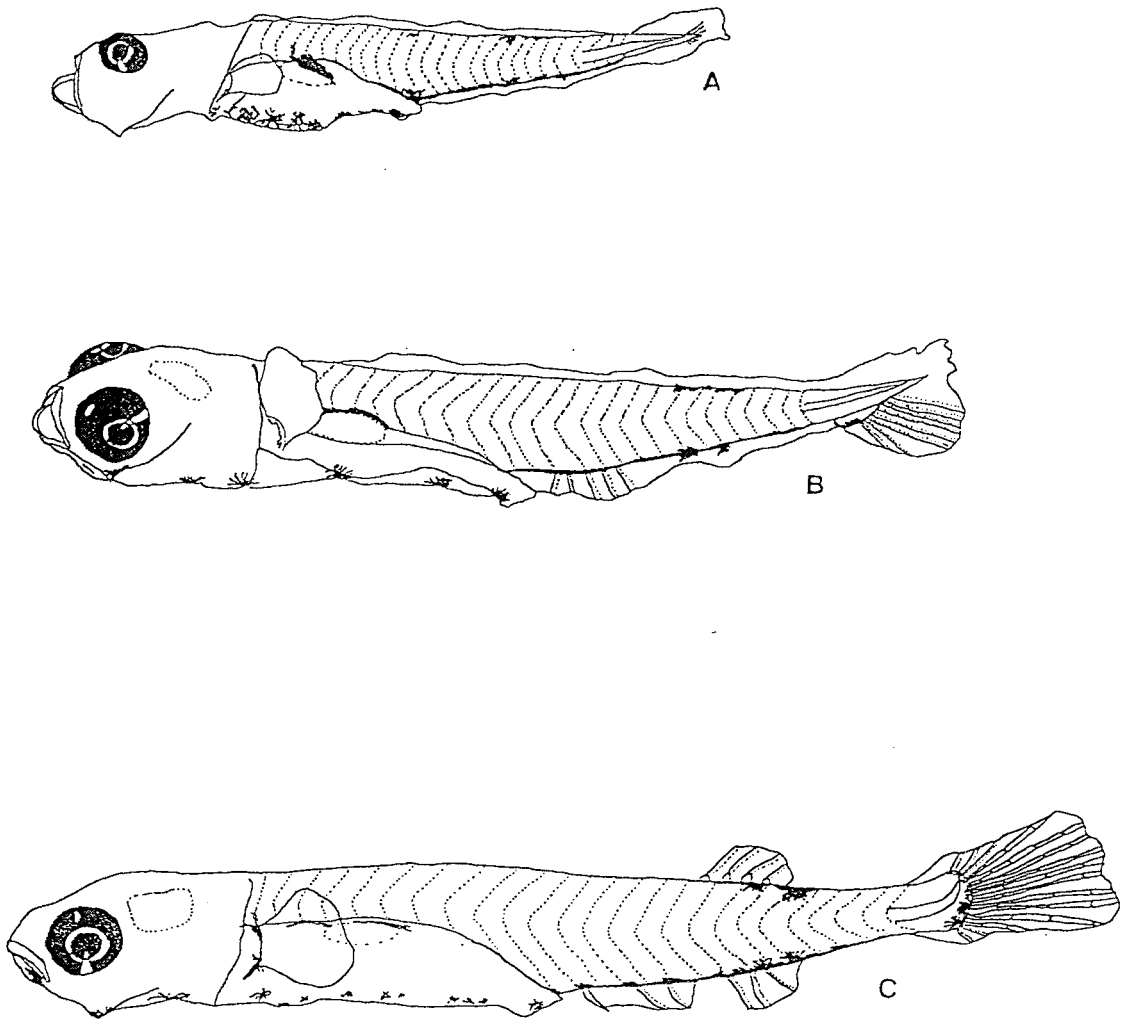


Figure 4.23 - Larvae of the unidentified gobiid, Species 1, from the south-east coast of South Africa. A: Stage - preflexion; BL - 3.56 mm; myomeres - 25 (10 + 15). B: Stage - preflexion; BL - 4.51 mm; myomeres - 25 (10 + 15); 25 vertebrae. C: Stage - flexion; BL - 5.81 mm; myomeres - 25 (9 + 16); 27 vertebrae.

Gobiidae Species 2 (Figure 4.24)

Morphology (Table 4.1) - Description is based on 15 preflexion and flexion larvae ranging in size from 2.13 to 4.85 mm BL. Larvae are moderately elongate, round to ovoid in cross section, and reasonably deep bodied. There are 27 (11-13 + 14-16) preflexion myomeres and 26 (12 + 14) flexion myomeres. Flexion is attained at approximately 3.8 mm BL. The gut is robust and straight, extending up to 64% BL. The gas bladder is large and conspicuous over the foregut region. The head is moderately large with a gently sloping rounded profile at first which becomes slightly concave at the flexion stage. The mouth is moderately large reaching as far as midpupil in the larger specimens. Numerous teeth are visible in both jaws in flexion larvae. The eye is moderately large and round. The pectoral fin bud forms early on, but no elements had differentiated, even in the largest specimens. The caudal fin anlage is visible soon after flexion with nine incipient rays having differentiated by 4.6 mm BL. The finfold appeared complete in all larvae.

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.53 - 0.63	0.56 - 0.64
PDL	0.21 - 0.23	0.24 - 0.37
HL	0.21 - 0.26	0.28 - 0.31
SnL	0.12 - 0.16	0.14 - 0.16
ED	0.09 - 0.11	0.12 - 0.13
BD	0.21 - 0.28	0.28 - 0.35

Pigment - All larvae bear head pigment at the dentary/premaxilla convergence, the angle of the lower jaw, the cleithral symphysis and over the hindbrain in the form of one or two stellar melanophores. Early preflexion larvae also have traces on the snout in front of the eye and along the lower jaw, while flexion specimens have a scattering of small melanophores beneath the lower jaw. Ventral gut pigment is extensive, comprising numerous stellar melanophores and pigment traces over the fore- and mid-gut surfaces and a narrow band over the hindgut region. The number of stellar melanophores decrease with size, but also move posteriorly while the narrow midline band progresses anteriorly until it covers the isthmus midline in the larger specimens. Pigment over the dorsal surface of the gut and air bladder is an extensive mixture of stellar melanophores along a broad pigment band. This band extends out over the ventral midline of the tail to beyond the final myoseptum with a few melanophores or narrow bands intruding onto the ventro-lateral surface. Medio-lateral tail pigment is also present, but the degree of cover is highly variable. Dorsal midline

pigment comprises a band covering the 6th to the 14th myomeres at early preflexion. Just prior to flexion this pigment breaks up and is distributed more dorso-laterally from behind the cleithrum to the 30th myoseptum. Flexion larvae bear four large pigment patches along the dorsal midline. A grouping of two to three large stellar melanophores are located along the lateral midline anterior to the final myoseptum.

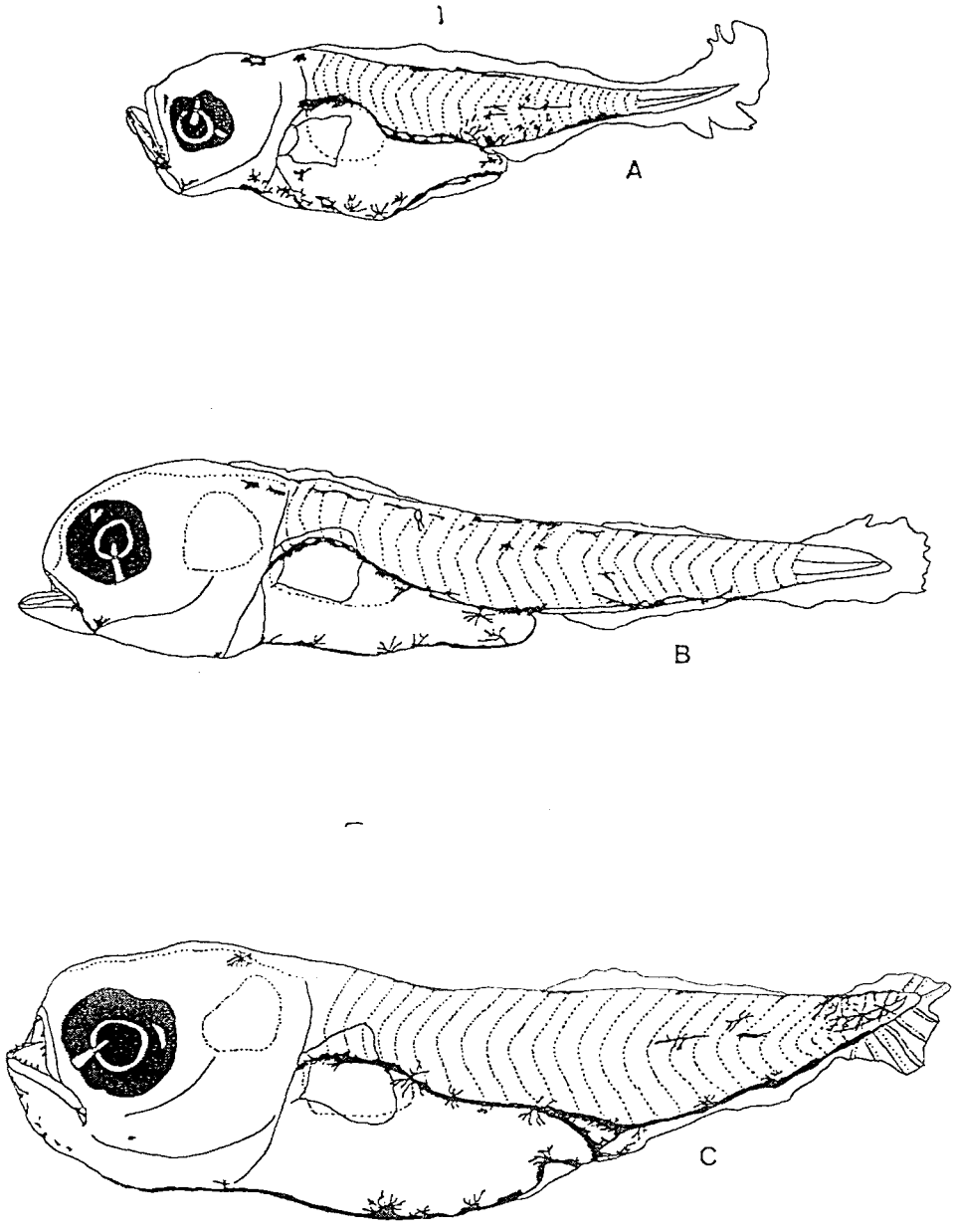


Figure 4.24 - Larvae of the unidentified gobiid, Species 2, from the south-east coast of South Africa. A: Stage - preflexion; BL - 2.15 mm; myomeres - 27 (13 + 14). B: Stage - preflexion; BL - 3.32 mm; myomeres - 27 (11 + 16). C: Stage - flexion; BL - 4.60 mm; myomeres - 26 (12 + 14).

Gobiidae Species 3 (Figure 4.25)

Morphology (Table 4.1) - Description is based on 18 preflexion and flexion larvae ranging in size from 2.61 to 7.23 mm BL. Larvae are moderately elongate, round to ovoid in cross section, and reasonably deep bodied. Postanal myomeres in preflexion larvae were not distinct, but there were 10 preanal myomeres visible. Flexion larvae had 24-26 (9-11 + 13-15) myomeres. Flexion of the notochord occurs at around 4.0 mm BL. The gut is straight, becoming deeper and more robust with size, and extends up to 66% BL. The gas bladder is large, but due to heavy pigment is visible in only a few specimens. The head is moderately large with a gently sloping rounded profile. The mouth is small and just reaches the anterior margin of the eye. Teeth are visible in the upper and lower jaw in flexion larvae > 5.0 mm BL. The eye is moderately large and round. The pectoral fin bud forms early on, but no elements differentiate until after 6.0 mm BL, with 19 incipient rays visible in the largest specimen. The caudal, anal and dorsal fin anlagen are all present by 4.0 mm BL with 4 + 5, five and three incipient rays respectively. By 5.9 mm BL there are 5 + 10 incipient dorsal rays, seven anal fin rays, 5 + 7 incipient primary caudal fin rays, and pelvic fin buds with five incipient rays. The largest larva had 6 + 9 and seven dorsal and anal incipient rays respectively, and five pelvic fin rays. The caudal fin had 6 + 5 fully developed primary rays and 6 + 5 incipient secondary rays. The finfold starts to break down soon after flexion and the appearance of the fin anlagen.

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.56 - 0.61	0.55 - 0.66
PDL	0.28 - 0.36	0.28 - 0.41
HL	0.28 - 0.33	0.30 - 0.33
SnL	0.17 - 0.21	0.16 - 0.18
ED	0.09 - 0.11	0.10 - 0.11
BD	0.25 - 0.27	0.25 - 0.30

Pigment - This species is heavily pigmented. The description of pigmentation that follows refers to preflexion larvae and flexion larvae < 6.0 mm BL. A characteristic feature of most larvae is the narrow band of pigment along the lateral midline of the head, starting on the snout and appearing to run through the eye and to the cleithrum. Pigmentation on the upper and lower jaws, at the angle of the lower jaw and along the ventral half of the inner preoperculum, and on the isthmus is prominent. The midbrain is extensively covered with stellar melanophores, with a few over the

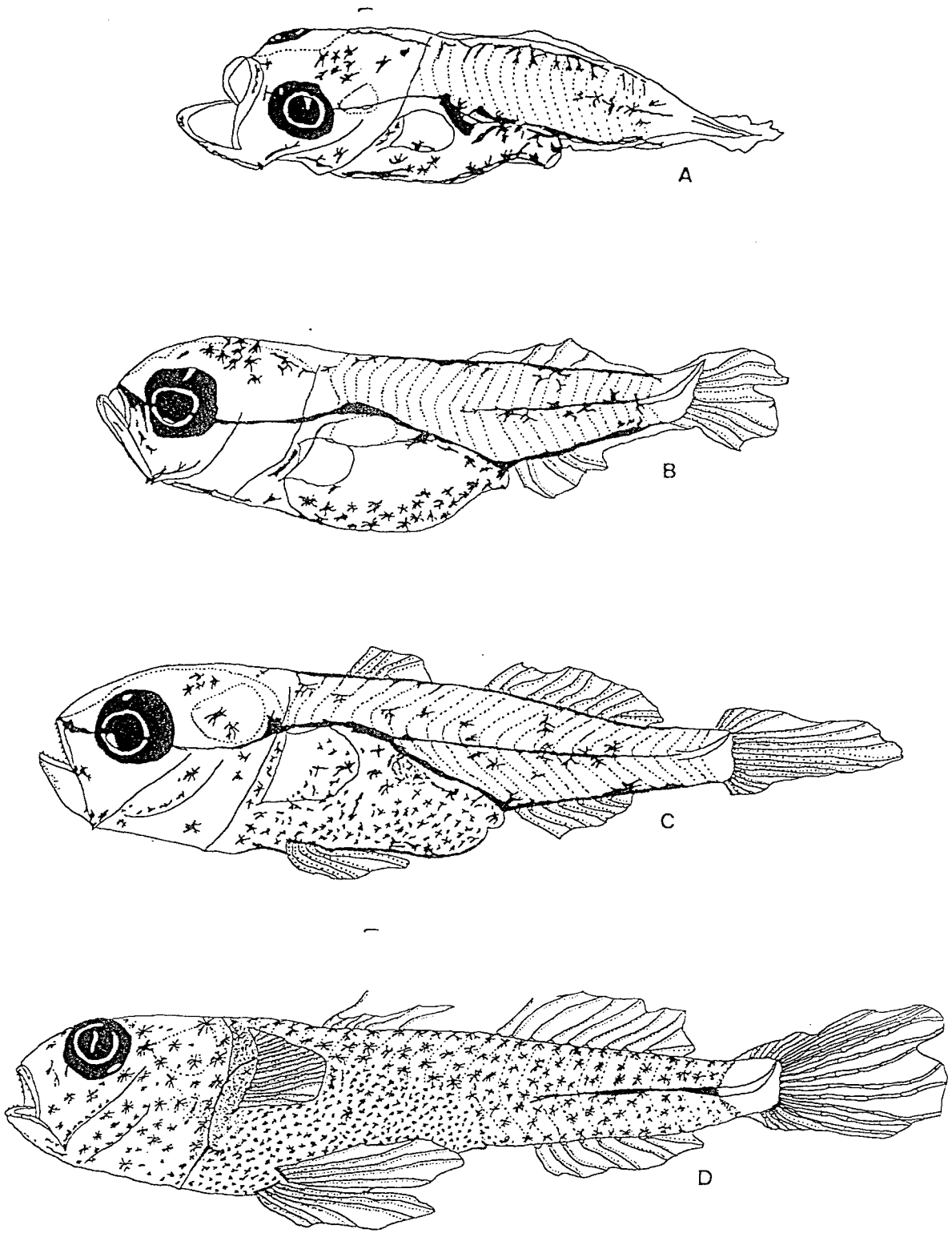


Figure 4.25 - Larvae of the unidentified gobiid, Species 3, from the south-east coast of South Africa. A: Stage - preflexion; BL - 2.61 mm; myomeres - not distinct. B: Stage - flexion; BL - 4.01 mm; myomeres - 24 (11 + 13). C: Stage - flexion; BL - 5.92 mm; myomeres - 24 (9 + 15); 27 vertebrae. D: Stage - flexion; BL - 7.21 mm; myomeres - 26 (11 + 15); 27 vertebrae.

hindbrain as well. The pectoral fin base is pigmented in all larvae. Ventral and ventro-lateral gut pigment is extensive and comprises mostly stellar melanophores but a few broad streaks in preflexion and early flexion larvae. The dorsal surface of the gut in these smaller specimens is almost completely covered by a dark band of pigment with a few narrower bands and patches intruding onto the dorso-lateral surface. In larger flexion larvae the dorsal and ventral midline surfaces are covered by a narrow band, but the rest of the gut is covered with densely packed pigment of various shapes and sizes. Ventral midline tail pigment is extensive and heavy in all larvae, with medio-lateral pigment becoming more prevalent with size until it seems to join with the dorsal gut pigment band in larger flexion larvae. Dorsal midline pigment is also prominent over the trunk and tail with intrusions along some of the myosepta onto the dorso-lateral surfaces. A scattering of stellar melanophores begins to cover the lateral surfaces of the trunk and tail in > 5.0 mm BL larvae.

The few larger > 7.0 mm BL flexion larvae were almost entirely covered in stellar melanophores. Traces of pigment still cover the upper jaw and region beneath the lower jaw, while small melanophores mark the anterior margins of the inner and outer preopercle. The entire peritoneal region is covered by densely packed stellar and y-shaped small melanophores. A broad band of pigment extends along the lateral midline from the 4th postanal myomere to the final myoseptum. The ventral half the cleithrum is marked by a narrow band of pigment which branches off toward the pectoral fin base. Small, densely packed pigment spots mark the region between the pectoral base and the cleithrum as well as the posterior margin of the final myoseptum. The remainder of the body, as far as the final myomere, is covered with large stellar melanophores, with the greatest density over the tail section.

Gobiidae Species 4 (Figure 4.26)

Morphology (Table 4.1) - Description is based on a single 5.82 mm BL flexion larva. Body elongate and round in cross section. There are 26 (9 + 17) myomeres. The gut is straight and reasonably robust, extending to 56% BL. The head is moderately large with a gently sloping rounded profile which becomes convex towards the tip of the snout. The mouth is small and reaches past the anterior margin of the eye which is moderately large and round. The pectoral fin bud is formed, but there are no visible rays. The caudal, anal and dorsal fin anlagen are all present. The caudal fin has 6 + 5 fully developed primary rays and 6 + 5 incipient secondary rays. Dorsal and anal fin counts are DVI+I, 10 and AI, 11. These two counts match those of adult *Oligolepis*

acutipennis, but it is possible that fin formation is not yet complete in this larva as the dorsal and anal rays are still incipient. The pelvic fin bud is present and possesses one spine and four elongate incipient rays.

Morphometrics (as a proportion of body length):

	Flexion larvae
PAL	0.56
PDL	0.38
HL	0.24
SnL	0.14
ED	0.09
BD	0.17

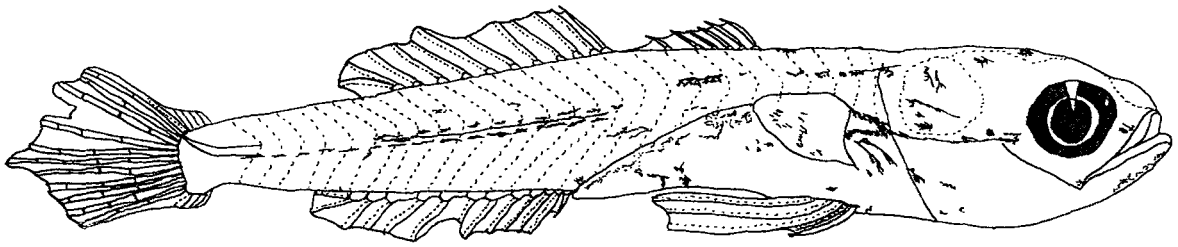


Figure 4.26 - Larva of the unidentified gobiid, Species 4, from the south-east coast of South Africa. Stage - flexion; BL - 5.82 mm; myomeres - 26 (9 + 17); 30 vertebrae.

Pigment - There are traces of pigment beneath the lower jaw, on the angle of the lower jaw, immediately in front of the eye, on the isthmus, the ventro-lateral operculum surface and the otic capsule. Two small stellar melanophores are located over the midbrain. A narrow band of pigment is located along the lateral midline from behind the eye to the cleithrum where it splits into two to finish at the base of the pectoral fin. Two more narrow pigment traces are located on the medio-lateral surface of the foregut. Two small pigment spots are visible at the base of the pelvic fin bud with traces on the pectoral fin membrane. A few patches of pigment can be seen on the lateral surface of the hindgut, while the dorso-ventral surface of the gut has numerous fine spots. There is medio-lateral pigment over the entire length of the tail, but it is heaviest from the vent to the 11th

postanal myomere. Dorso-ventral pigment marks the trunk region over most of the preanal myomeres.

Similar species - According to Leis & Trnski (1989) only larvae from the Apogonidae, Eleotridae and Scaridae can be confused with gobiid larvae. Apogonids, however, are generally deeper bodied with a shorter, coiled gut, preopercular spination and larger size at flexion. Eleotrids are mostly confined to freshwater and estuaries. The few that are found in the sea in southern Africa are confined to subtropical and tropical waters (Hoese 1986), ruling out their occurrence in the cool temperate south east coastal waters. Narrow or square-shaped eyes separate preflexion scarids from similar sized gobiids.

The goby species, *Lesueurigobius sanzoi* (Olivar 1989), *Sufflogobius bibarbatus* (O'Toole 1978b) and *Psammogobius knysnaensis* (Melville-Smith 1978), whose larvae from southern African waters have been described, as well as the four dealt with here differ markedly from each other. Despite all of them displaying the general morphological and morphometrical characteristics of gobiid larvae, a combination of the heaviness and distribution of pigmentation, size at flexion, and number and ratio of myomeres separate them easily. In addition, both *L. sanzoi* and *S. bibarbatus* have southern African distributions restricted to the west and upper west coasts (Miller 1986; Hoese 1986), and the chances of larvae being found this far up the east coast are slight.

Family - Cynoglossidae

Cynoglossus zanzibarensis Norman, 1939 (Figure 4.27)

Morphology - Description is based on 35 preflexion and flexion larvae ranging in size from 2.42 to 16.3 mm BL. Preflexion larvae are elongate, moderately compressed and bilaterally symmetrical. After flexion they become deeper bodied, especially around the head and trunk section, and very compressed. Larvae up to 3.4 mm BL still bear remnants of a yolk-sac with numerous small, densely concentrated oil globules. There are 46-57 (6-9 + 37-50) myomeres. The gut is short, coiled and compact, extending to 37% BL in preflexion larvae and 32% BL in flexion larvae. It also protrudes well below the ventral level of the body margin. The anus projects to the right of the midline behind the origin of the anal fin. The head is small with a short, rounded snout. The formation of the rostral hook begins soon after flexion, and after eye migration quickly covers the snout to well past the anterior margin of the mouth. The mouth reaches as far back as the posterior margin of the pupil. Small teeth are visible by 4.5 mm BL and become more numerous

and finer with development. The eye is small and round with a small projection from the posterior margin. Migration of the right eye over to the left side of the head was initiated in larvae > 14.5 mm BL and complete by 16.3 mm BL. Flexion was initiated in some larvae as early as 5.6 mm BL, with all larvae > 6.78 mm BL having undergone flexion. A pectoral fin bud and membrane are present, but no rays ever differentiate. The pectoral bud is lost late during flexion, soon after eye migration. The dorsal and anal fin anlagen appear at about the same time, with two elongate dorsal rays becoming visible at approximately 3.5 mm BL. The first two incipient rays of the dorsal fin in this species are elongate, but are reduced during late flexion when they become the shortest of the dorsal rays. The single medial pelvic fin bud appears by 6.23 mm BL. The fin element count in the largest specimen was D123; A102; PV5; C9. Remnants of the finfold are still visible after flexion and before the appearance of the first incipient caudal fin rays.

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.30 - 0.37	0.27 - 0.32
PDL	0.04 - 0.07	0.006 - 0.02
HL	0.17 - 0.18	0.18 - 0.21
SnL	0.08 - 0.09	0.07 - 0.10
ED	0.05 - 0.06	0.03 - 0.05
BD	0.24 - 0.28	0.23 - 0.34

Pigment - Yolk-sac larvae have faint traces of pigment at the angle of the lower jaw, on the operculum and over the hindbrain. A few small melanophores are visible on the lateral surface of the foregut and ventrally on the mid- and hind-gut beneath the remnant yolk-sac. The dorsal and ventral midlines of the tail are covered by a longitudinal series of small melanophores which run almost to the tip of the notochord. The finfold is dotted with small scattered pigment spots. Small preflexion specimens display a move of pigment from the hindbrain to the midbrain, and traces are evident on the isthmus and preoperculum. Head pigmentation is otherwise the same as for yolk-sac larvae. Ventral and lateral gut pigment, comprising small spots and patches, is heavier and more widespread than earlier. Dorsal and ventral midline pigment on the tail is similar, extending a bit further towards the notochord tip, and now includes the dorsal section of the trunk. A few pigment marks appear on the medio-lateral surface of the trunk above the gut. The finfold still bears isolated groups of melanophores. The larger preflexion specimens still have trace pigment at the lower jaw angle, and on the surfaces of the preoperculum, operculum and mid- to hind-brain area. Additional

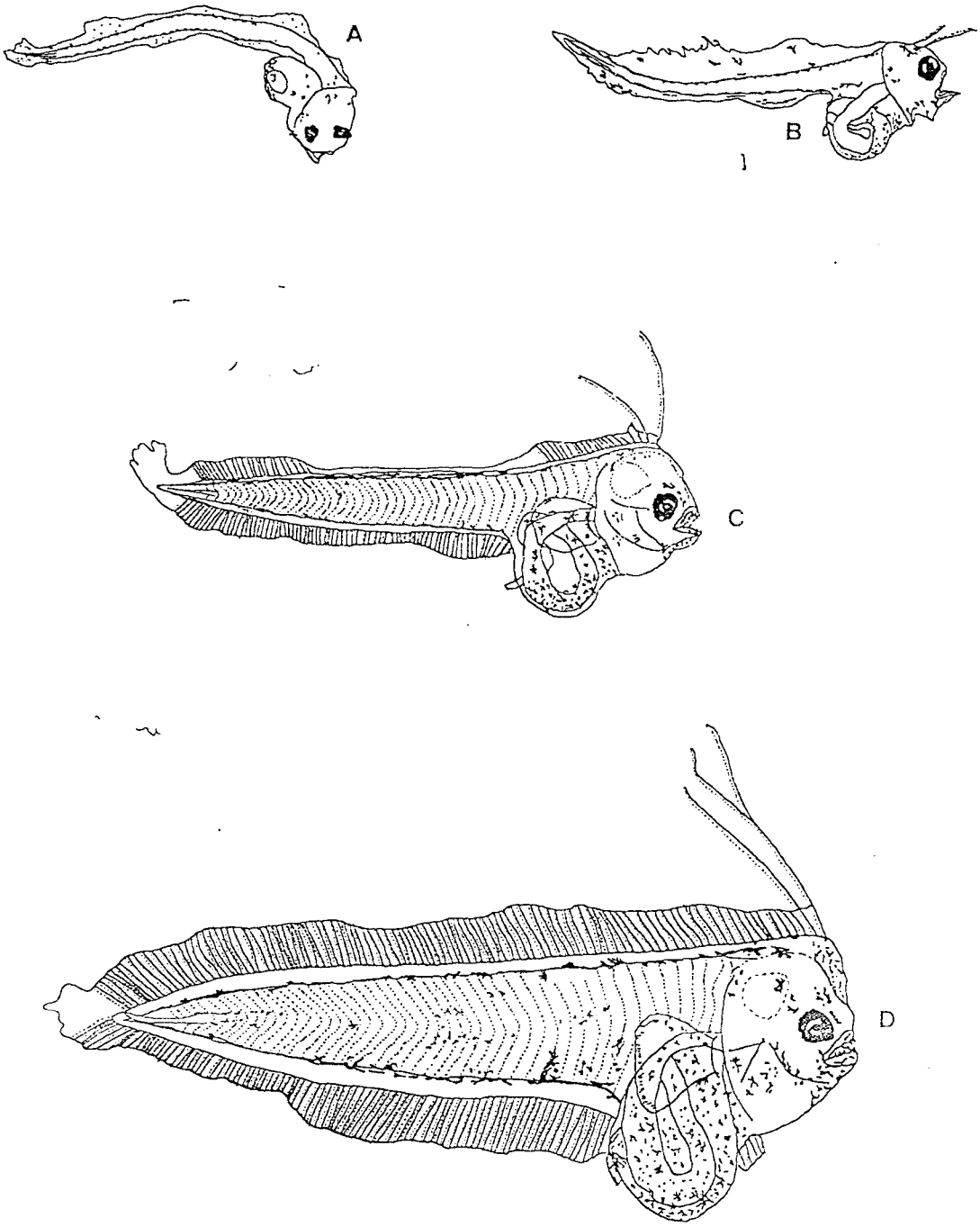


Figure 4.27 - Larvae of the cynoglossid, *Cynoglossus zanzibarensis* Norman, 1939, from the south-east coast of South Africa. A: Stage - preflexion; BL - 3.35 mm; myomeres - not distinct. B: Stage - preflexion; BL - 3.74 mm; myomeres - not distinct. C: Stage - preflexion: BL - 5.78 mm; myomeres - 46 (9 + 37). D: Stage - flexion; BL - 6.41 mm; myomeres - 48 (8 + 40).

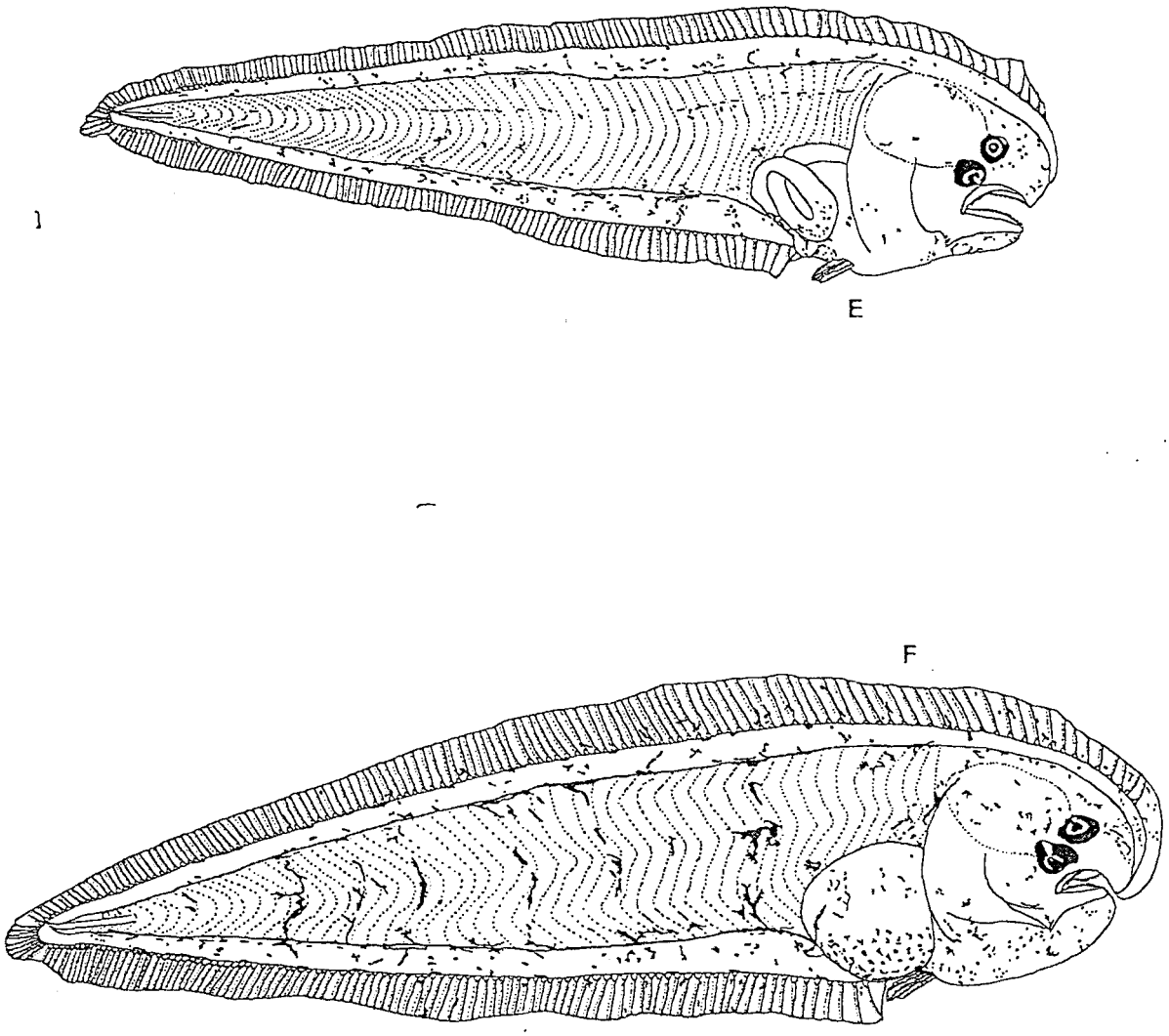


Figure 4.27 (continued) - Larvae of the cynoglossid, *Cynoglossus zanzibarensis* Norman, 1939, from the south-east coast of South Africa. E: Stage - flexion; BL - 11.62 mm; myomeres - 56 (6 + 50); 61-63 vertebrae. F: Stage - flexion; BL - 15.10 mm; myomeres - 57 (10 + 47).

pigment is visible on both jaws, beneath the lower jaw and on the snout just anterior to and above the eye. There is little change in the ventral and lateral gut pigment except that now it mostly comprises small stellar melanophores. The pectoral fin membrane also bears a mixture of stellar melanophores and pigment patches. Early flexion larvae have considerably more head pigment, with both jaws, the surface beneath the lower jaw, the snout, mid- and hindbrain, otic capsule,

preoperculum and operculum all bearing some degree of coloration. The rostral hook arising from near the anterior section of the dorsal fin anlage is peppered with small pigment spots. Pigmentation on the gut has expanded to include the dorsal section as well, and the pectoral fin is heavily covered. Midline tail and trunk pigmentation is similar to that seen in late flexion specimens, except that it is heavier and extends right to the notochord tip. Some melanophores and patches overlap onto the caudal and anal fin anlagen as well as the dorso- and ventro-lateral surfaces. Groupings of medio-lateral pigment are to be found on the tail as far back as the 34th postanal myomere. Head pigment is quite extensive in the larger flexion larvae, covering most surfaces including the rostral hook, but it is light compared to that seen on smaller flexion specimens. Dorsal pigment on the gut is also reduced. Midline pigment on both dorsal and ventral surfaces of the trunk and tail still covers from the nape to the tip of the notochord, but is not as dark. The dorsal and anal fin anlagen are more extensively covered than before. Six vertical bars of pigment begin to form on the tails of larger larvae with small groups of dorso- and ventro-lateral pigment still present. The base of each dorsal, anal and caudal fin ray is marked by a very small, faint melanophore. The fin membranes also bear a scattering of melanophores.

Similar species - Amongst those families whose early developmental stages could be confused with the cynoglossids are the carapids, some ophidioids and other pleuronectiforms (Leis & Trnski 1989). However, closer examination will reveal that carapid larvae have a higher myomere count, no elongate ray on the head and no caudal fin, while the ophidioids have flesh-like protuberances on the gut, more myomeres, paired pelvic fins, no elongate dorsal rays, and pectoral fins with rays. As for distinguishing cynoglossids from other flatfish species, a host of characters including myomere totals and ratios, pectoral fin shape, fin ray counts, extent of gut protrusion, mouth size, eye size and shape, head spination, and pigment patterns can all be used in the process.

The larvae of *Cynoglossus capensis* have previously been described by Brownell (1979). Both *C. capensis* and *C. zanzibarensis* occur within the study area (Heemstra 1986d), but their larvae can be distinguished by their unique pigment patterns, fin element counts in late flexion specimens (fewer in *C. capensis*), size at flexion and metamorphosis (smaller in *C. capensis*) and the number of elongate dorsal rays (*C. capensis* may have between two and four, while *C. zanzibarensis* only ever has two). In addition, the appearance of the elongate dorsal rays occurs at a smaller size in *C. zanzibarensis*.

Family - Soleidae

Austroglossus pectoralis (Kaup, 1858 - Figure 4.28)

Morphology - Description is based on 22 larvae ranging in size from 1.6 mm to 8.8 mm BL. The majority (20) of these were flexion specimens as preflexion larvae were not as abundant and were easily damaged during the clearing and staining process. Larvae are not very elongate, are laterally compressed, bilaterally symmetrical until eye migration, and are only moderately deep bodied, the gut however, is massive and protrudes well below the ventral margin of the body. Myomere counts were not possible for the few preflexion larvae examined, with only eight preanal myomeres visible in some, but ranged from 48-52 (8 + 40-44) in flexion specimens. The smallest larva (1.6 mm BL) possessed a yolk-sac, with those < 2.9 mm BL still displaying remnants of yolk. Flexion in this species is evident in some 3.5 mm BL larvae, and in all those > 3.8 mm BL. The largest specimen (8.8 mm BL) was still undergoing flexion. The gut is coiled, extending to 52% BL in preflexion larvae and 42% in flexion larvae. This anterior movement of the gut as development progresses is typical of all soleid larvae (Leis & Trnski 1989). The head is moderately large with a steep profile during initial stages and a more gradual convex profile in later stages. The mouth becomes relatively larger during flexion, eventually reaching the posterior margin of the eye in the largest specimens. Small, robust teeth are visible in all flexion larvae, with those in the lower jaw becoming elongate and incisor-shaped in the larger larvae. The eye is small and round. There was no evidence of eye migration in any of the larger flexion specimens examined. Pectoral fin buds are visible from the early preflexion stage, but no rays develop. The caudal fin anlage is the fist to appear, followed by the dorsal and anal anlagen. Large flexion larvae had a percentage of fully developed caudal fin rays, but fin element formation was far from complete and the dorsal, anal and caudal fin membranes are still fused. An 8.67 mm BL larva has a fin count of D92; A86; C7. A translucent zone develops dorsal to the body musculature in late flexion larvae and houses the elongate dorsal pterygiophores.

Morphometrics (as a proportion of body length):

	Preflexion larvae	Flexion larvae
PAL	0.48 - 0.52	0.40 - 0.42
PDL	0.17 - 0.21	0.05 - 0.11
HL	0.36 - 0.41	0.24 - 0.28
SnL	0.10 - 0.11	0.09 - 0.13
ED	0.04 - 0.05	0.02 - 0.05

BD 0.45 - 0.51 0.32 - 0.41

Pigment - Preflexion larvae are heavily pigmented. Large patches of pigment are visible over the fore- and mid-brain and on the snout in front of the eye. Three to four spots are found beneath the lower jaw while the angle of the lower jaw is extensively covered. Isolated patches are evident on the subopercular and opercular surfaces. Two melanophores are found on the anterior margin of the cleithrum near to the hindbrain. Large stellar melanophores are distributed along the ventral and ventro-lateral surfaces of the gut. The dorsal midline of the gut bears a narrow band which is punctuated by two larger patches over the anterior portion. The ventral midline of the tail bears 18 large melanophores packed closely together in a longitudinal series which extends to just short of the notochord tip. Arising from some of these melanophores are branches of pigment which intrude onto the lateral surface of the tail. Eleven large melanophores mark the dorsal midline of the trunk and tail, with some overlapping onto the finfold and some sending out branches onto the lateral surface. Three smaller melanophores are arranged over the notochord tip. Much of the finfold is pigmented. The head pigmentation on flexion larvae still comprises coverage of the midbrain, snout, lower jaw surface and angle and operculum. The single large stellar melanophore on the operculum in smaller flexion specimens is lost and the degree of coverage beneath the lower jaw and on the snout decreases in large flexion larvae. The pectoral fin membrane bears a few patches and branches of pigment in no specific pattern. Gut pigment is still largely restricted to the ventral and ventro-lateral surfaces in the form of large stellar melanophores and irregular branches. Dorsal gut pigment is much reduced from what was evident in preflexion larvae. There are 15 - 17 large melanophores along the ventral midline of the tail, some of which have branches stretching onto the ventro-lateral surface. The larger flexion specimens have a single vertical pigment patch immediately posterior to the vent. Twelve to fourteen medium to large melanophores straddle the dorsal midline of the trunk and tail, with the spacing between them increasing with larval size so that they extend almost to the notochord tip in late flexion larvae. Some of these melanophores overlap onto the dorsal translucent zone and the dorso-ventral surface. The small melanophores near the notochord tip in preflexion specimens have been lost by the time notochord flexion is initiated. A single medium-sized stellar melanophore is situated medio-laterally on the 11th postanal myoseptum in larger flexion stages. The dorsal translucent zone bears small groups of trace pigment, while the anal fin membrane is marked in a few places.

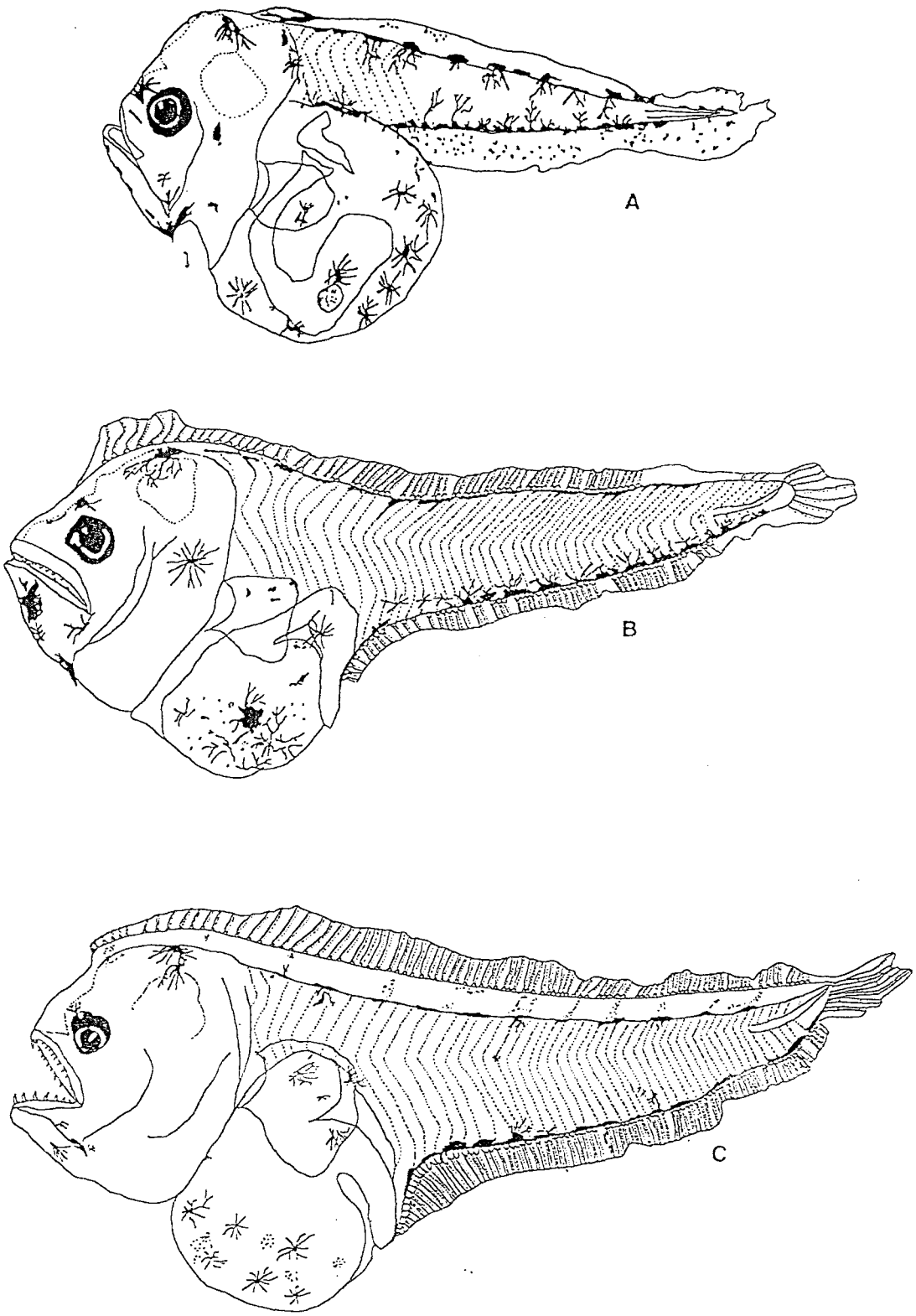


Figure 4.28 - Larvae of the soleid, *Austroglossus pectoralis* (Kaup, 1858), from the south-east coast of South Africa. A: Stage - preflexion; BL - 2.90 mm; myomeres - not distinct. B: Stage - flexion; BL - 4.91 mm; myomeres - 48 (8 + 40). C: Stage - flexion; BL - 8.67 mm; myomeres - 52 (8 + 44); 52 vertebrae.

Similar species - According to Leis & Trnski (1989) the suite of characters which is used to describe soleid larvae are unique amongst the flatfishes, and as such they are not susceptible to misidentification. Amongst these characters are the absence of elongate fin rays, a convex head profile, no head spination, large gut, small eyes, a pectoral fin which is not paddle-shaped and which is retained through metamorphosis, and paired pelvic fins.

The larval descriptions of six soleid species found in southern African waters have been published, namely *Austroglossus microplepis* (O'Toole 1977a; Brownell 1979), *Buglossidium luteum* (Nichols 1976 in Olivar & Fortuño 1991), *Dicologlossa cuneata* (Lagardère & Aboussouan 1981 in Olivar & Fortuño *op. cit.*), *Heteromycteris capensis* (Melville-Smith 1978; Brownell *op. cit.*), *Monochirus ocellatus* (Palomera & Rubiès 1977 in Olivar & Fortuño *op. cit.*), *Solea bleekeri* (Melville-Smith *op. cit.*) and *Synapturichthys kleini* (Brownell *op. cit.*). The most obvious differences between these species and *A. pectoralis* encompass myomere counts and ratios, pigment patterns, size at flexion, and fin counts. The closely related *A. microlepis* is not as heavily pigmented, has fewer dorsal and anal fin rays, and attains flexion at a larger size (5.2 mm SL - O'Toole *op. cit.*). In addition, its distribution is restricted along the west coast and as far as False Bay (Heemstra & Gon 1986), whereas *A. pectoralis* is distributed from the Cape all along the east coast to Natal.

These descriptions are seen as a vital contribution towards the future research efforts into ichthyoplankton along the south-east coast of South Africa. However, the descriptions of many of these species are still incomplete and based only on a few specimens or single developmental stages. The process of illustrating and describing these and other new species will be an ongoing one as long as research into the early life history stages of fishes along our coastline is continued.

CHAPTER 5 - AN ICHTHYOPLANKTON CHECKLIST FOR THE SOUTH-EAST COAST, AND THE USE OF SPATIAL AND TEMPORAL DISTRIBUTIONAL PATTERNS OF LARVAE IN CONFIRMING AND DETERMINING ADULT SPAWNING BEHAVIOUR AND TIMING

INTRODUCTION

Perhaps the most important underlying reason for the study of temporal and spatial ichthyoplankton distributions is the monitoring of factors affecting the various early life history stages which may determine cohort strength and recruitment (Saville & Schnack 1981) and ultimately the available stock to fishers. Since the original concept of biomass estimation via the Daily Egg Production Method (DEPM; Saville 1964), which assumes that the daily production of eggs by a stock is proportional to its spawner biomass (Somerton, Kobayashi & Landgraf 1993), it has been frequently used as an aid to fisheries management (Parker 1980; Armstrong, Shelton, Hampton, Jolly & Melo 1988; Alheit 1993; Priede & Watson 1993). Since the summer of 1984 the DEPM has been used as a tool to help determine Total Allowable Catches (TAC's) along the west coast of South Africa for *E. japonicus* and *S. sagax* respectively (Le Clus & Malan 1995; Shelton, Armstrong & Roel 1993). While this method characteristically provides estimates with high variance, when used in combination with hydro-acoustic methods (HAM - see Hampton, Armstrong, Jolly & Shelton 1990; Roel, Hewitson, Kerstan & Hampton 1994), results are more reliable (Bergh & Butterworth 1987; Shelton *et al. op. cit.*). Prior to the introduction of DEPM and HAM into the management process in the pelagic fishery, the TAC for *E. japonicus* between 1972 and 1985 was set at a constant, and catches were stable (Cochrane & Starfield 1992). Subsequent to the introduction of these techniques which led to a better understanding of the spawner biomass/recruit relationship, catches have varied significantly - most notably between 1987 and 1991 with TAC's being based partly on the data gleaned from surveys utilising DEPM's and HAM's.

Abundance estimates from ichthyoplankton surveys can also be taken as a measure of the spawning potential of a stock and of mortality rates (Conand 1981; Shelton & Hutchings 1981), and be related to catch per unit effort as an index for future predictions about yield. In the case of the *Sardinella aurita* fishery off Dakar, North West Africa this technique proved useful for a stock where fishery statistics are incomplete. Based on the number of stage 1 eggs caught during the 1977 spawning season and fecundity estimates, the size of the Western spawner stock for *Scomber*

scombrus was estimated and used to recommend a TAC for the following year (Lockwood, Nichols & Dawson 1981). However, there are always exceptions, e.g. larval survival and catch rates of *Clupea harengus* along the coast of Maine often compared well with subsequent spring harvest levels in the juvenile herring fishery, but a poor catch in 1971 followed very high larval survival rates and catches the previous winter (Graham 1980).

Temporal Distribution

Fundamental to this type of work are the studies which initially determine the whereabouts of eggs and larvae of target species and ascertain seasonal trends in abundance and distribution, elements which are of concern to elementary research on the dynamics of planktonic communities. Tied in with this would be the close association between the presence of ichthyoplankton and adults, whose spawning habits (timing and location) may also ultimately determine the fate of their water borne propagules as stated in the herring hypothesis of Iles & Sinclair (1982). Observations on the distribution and abundance of fish eggs and larvae go a long way to provide a better understanding of a species' biology and ecology (Doyle, Rugen & Brodeur 1995) and help uncover links between life history strategies and the environment. A consistent spawning pattern from year to year for *E. japonicus* in South Africa's Benguela system which ensured transport of larvae to nutrient rich waters, thereby ensuring high survival rates, good recruitment and relatively accurate yield predictions is part of the reason attributed to the absence of large-scale fluctuations in this fishery during the 1970s (Shelton & Hutchings 1981). Peaks in *Brevoortia tyrannus* egg densities in the New York area reflected spawning peaks and a shift in spawning sites (Ferraro 1981) which were related to the following of optimal temperatures by the spawner stock. Seasonal changes in dominant species can be linked to spawning cycles or transport of larvae away from the sample area, e.g. low overall numbers of larvae on Georges Bank in the 1976/77 season were explained by the unusual strong northwest winds that year which set up an Eckman transport pattern which carried larvae away from the area (Bolz, Lough & Potter 1981). Routine sampling over a period of years can also reflect changes in community structure where previously dominant species have been ousted or reduced in numbers due to anomalous conditions. e.g. the changing freshwater fish community in the upper half of the Ohio River which was reflected in larval catches between 1976 and 1978 (Burch, Margulies, Clark, Fini & Huff 1981). Detection of different spawning grounds or seasons, from ichthyoplankton surveys, for closely related species such as the bothids on the

Florida shelf (Dowd 1981) may well point to an evolved mechanism for reduced competition and a decrease in density dependent mortality.

Spatial Distribution

While recruitment in fishes is a process which is poorly understood, it is frequently used to explain the fluctuations in population or stock sizes. However, it also has meaning outside of the fisheries context in that it is fundamental to the continuation of a species (Okubo 1994). Increasingly, the goal of large surveys is the monitoring of inter- and intra-annual variation in ichthyoplankton abundance and mortality and how it is related to oceanography and recruitment processes (Morse 1989; Japp, Sims & Smale 1994; Verheye, Hutchings, Huggett, Carter, Peterson & Painting 1994). However, some believe the processes which determine recruitment strength begin with the reproductive strategy of adults (Cushing 1990a) which attempt to spawn in a place and at a time which will derive maximum benefit for their pelagic propagules. The transport or retention of eggs and larvae, and in certain cases juveniles, is what ultimately determines the success of recruitment as the early life history stages find themselves in favourable or hostile environments. An extreme situation regarding this is found amongst marine island populations which, by virtue of their isolation, rely on local recruitment (Boehlert, Watson & Sun 1992; Boehlert & Mundy 1993) which must be achieved in conditions characterised by oceanic currents more suited to dispersal. While temporal distribution is a reflection of the timing of spawning which is often linked to environmental conditions which favour survival (Choat, Ayling & Schiel 1988), it has been proposed that spatial patterns reflect a preference for specific settlement habitats by larvae. While the inshore region along the south-east Cape coast may not appear to be isolated in terms of an oceanic island or seamount (Boehlert & Mundy *op. cit.*), many species are restricted or endemic to this habitat and as such must too rely on recruitment back to this region for survival. In fact Leis (1993) suggests that distributional patterns of temperate rocky reef fishes may be similar to those observed for species originating from point source coral reefs, a sentiment backed up by findings in intertidal (Marliave 1986) and shallow coastal waters (Barnett, Jahn, Sertic & Watson 1984; Kingsford 1988). As the majority of these nearshore species spawn pelagic eggs, and almost all have pelagic larvae, the distance these propagules are found from the desired habitat and the mechanisms of retention are important considerations in the understanding of the species assemblage. The reproductive guild which a species occupies can

also influence the offshore distribution of the larvae. Species confined to the nearshore or intertidal zone provide some examples of the extreme kind where larvae are seldom found further than 500 metres away from prime settlement habitats or substrates (Jahn & Lavenberg 1986; Marliave 1986). Included amongst these are many larvae belonging to the Tripterygiidae, Bythitidae, Gobiesocidae and Gobiidae (Kobayashi 1989; Leis 1986 in Boehlert & Mundy *op. cit.*; Boehlert & Mundy *op. cit*), as well as selected clupeids and sciaenids (Powles 1977; Miller & Woods 1988). Although there are exceptions to this pattern and the idea does not have universal appeal (e.g. Clarke 1991), larvae of species from a coral reef assemblage with non-pelagic eggs generally decrease in abundance as one moves offshore from the point source, while those with pelagic eggs are either more abundant offshore or decrease less rapidly further from shore (Leis & Miller 1976; Leis 1993).

While investigating year class strength for *Merluccius productus*, Bailey, Francis & Mais (1986) stated that processes which occur during the first year of life ultimately determined cohort strength. Such processes include food availability, predation, sites of spawning, larval transport (dispersal or retention), and rates of development. In later studies it appeared that early and late larval stages were the phases during the first year which were most vulnerable to these processes and that transport to and retention in nursery areas, which are highly productive and hold large concentrations of their favoured prey item (*Calanus pacificus*), is the primary process determining year class strength (Hollowed 1992). In the case of *Engraulis mordax*, however, it was ascertained that cohort strength was determined during the early juvenile stages (Peterman, Bradford, Lo & Methot 1988) due to the vulnerability of this species at that stage to predation by a host of other sea animals. Egg and larval development and duration differs markedly between the hakes and anchovy fishes, with rates of development amongst the engraulids being much faster. This difference in life history characteristics means that hake larvae are vulnerable in the plankton for longer, but by the time they metamorphose they are strong and resilient to environmental change, and capable of evading capture, more so than the faster developing, but weaker anchovy.

Spawning and nursery areas for many species are separated by great distances (Harden Jones 1968 in Rijnsdorp, van Stralen & van der Veer 1985) and although the mechanisms of transport to and retention in nursery areas are poorly understood, they result in the observed

horizontal distributional patterns which can allude to the location of spawning sites and recruitment patterns. Due to buoyant eggs in many cases and the poor swimming abilities of the early larval developmental stages, distribution of these planktonic propagules is largely a result of adult spawning habits and local physical processes. Whether larvae are retained over habitats suitable for settlement after metamorphosis or initially dispersed away from them to be returned later, oceanographic processes are involved (see Roughgarden, Gaines & Possingham 1988; Okubo 1994). If larvae cannot be retained or returned to grounds favourable for settlement, closure of the life cycle cannot be completed and the animal is doomed.

The site and timing of spawning in adult fish and the behaviour or activity of larvae are considered by some to be the causal factors behind ichthyoplankton distributional patterns (Doyle 1989). These patterns of distribution and abundance can in turn be used to provide vital information on the life history of species (Judy & Lewis 1983). This kind of information can be difficult to obtain for certain species such as pelagic oceanic fish where extensive surveys need to be undertaken to sample the large areas of the world's oceans. For fishes with neritic and nearshore distributions the area which requires coverage is smaller, but the task is no less difficult. The close association of winter spawning in *B. tyrannus* and *Leiostomus xanthurus* and the Gulf Stream front (Govoni 1993) has led to the use of their eggs and newly hatched larvae as indicator species for this oceanographic feature. Serial sampling along a transect also showed that larvae of both species show a gradient of increasing size and age towards the shore (Judy & Lewis *op. cit.*; Lewis & Judy 1983; Warlen 1992) where late stage larvae enter estuaries to metamorphosize and spend their first year of life. In order for a species to survive, their life history must be compatible with the surrounding environment. Conditions such as prevailing currents, production cycles, temperature regimes, and upwelling (McGowen 1993) act on species which in turn must react. Within a geographic location it is inevitable that several species will adopt a similar strategy to ensure continuation of their line. For example, the spawning seasons of five commercially important species (*B. tyrannus*, *L. xanthurus*, *Micropogonias undulatus*, *Paralichthys lethostigma* & *Paralichthys dentatus*) off North Carolina coincide with currents which favour onshore transport of larvae. All species spawn offshore near the Gulf Stream and larvae are then transported up to 200 km inshore where they make use of estuaries as juvenile nursery areas (Miller, Reed & Pietrafesa 1984).

The larvae of *B. tyrannus* are pelagic and those of the other four more benthic orientated. Seasonal differences in the vertical placement of onshore currents and the correct timing of spawning are responsible for ensuring the larvae reach the safe haven of estuaries. Trends in onshore-offshore distribution with respect to larval densities and species have also been observed in the region of the Hawaiian islands and Lizard Island in the Great Barrier Reef, with passive advection being invoked to explain the offshore dispersal, and active swimming, epibenthic schooling and the use of favourable currents, such as mesoscale eddies and onshore water movement at discrete depths, being proposed as the mechanisms used by some species to ensure inshore retention (Leis & Miller 1976; Leis 1982; Kobayashi 1989; Leis, Goldman & Raeder 1989).

The distribution of ichthyoplankton on a micro-scale and how it is related to prevailing environmental conditions goes a long way to providing answers about regional differences in year-class strength, and is dealt with at a later stage in this thesis. The ichthyoplankton communities of the nearshore region along the South African coastline, in particular the south-east Cape, have not been studied extensively. Anders (1975). Beckley (1985; 1986; 1993). Harris (1996), Shelton & Kriel (1980) and Whitfield (1989c) have dealt with various aspects such as distribution and transport mechanisms and community structures in different zones. Along the south-eastern seaboard, specific work on the neritic ichthyoplankton west of Algoa Bay has been restricted to the initial survey carried out in the Tsitsikamma National Park (TNP - Tilney & Buxton 1994; Tilney *et al.* 1996) which provided the impetus for this program.

The aim of this section was firstly to add to the species checklist of the ichthyoplankton fauna in the south-east Cape and relate this to the known sub-adult and adult species assemblage. Secondly egg and larval presence (both temporal and spatial), sizes and concentrations are used to enhance the knowledge about adult spawning habits and larval distribution. This information will be used at a later stage when addressing the aspects dispersal and retention.

MATERIALS AND METHODS

Temporal Distribution

With the exception of the few occasions mentioned in Chapter 1, samples were obtained on a monthly basis between August 1993 and October 1996 using bongo nets and RMT1x6 multiple net

samplers operated from the boats *Natpark Aonyx*, R.S. *Algoa* and R.S. *Africana*. The sampling strategy was described in more detail in Chapter 1, and the handling and processing of all samples followed the protocol outlined in Chapter 2. All samples were used to enhance the ichthyoplankton database for the region as well as to track spawning seasons by monthly appearance of eggs, larvae and squid para-larvae. Ichthyoplankton and squid para-larval distribution patterns were related to known spawning times and habits of adults.

The body length (BL) of all larvae and dorsal mantle length of squid larvae were measured (to the nearest 0.1 mm) and the mean monthly sizes looked at in the context of spawning periodicity and larval retention. Not all specimens could be measured due to damage incurred during sampling and handling. Seasonal trends were analysed for those species which were present on more than four occasions in samples from the Middlebank region. In months where Middlebank was not sampled or when other sites were sampled in addition to Middlebank, total concentrations from all sites combined are also presented. The total concentrations each month for all species, eggs and squid para-larvae from Middlebank and from combined stations were also subjected to analysis. For this purpose months from the same season were grouped, irrespective of year and tested for similarity using the Kruskal-Wallis single factor analysis of variance by ranks at the 95% confidence level.

Spatial Distribution

Between January 1995 and May 1996 samples were taken from Middlebank and along an offshore transect at stations 5, 10 and 15 nautical miles (nm) off Storms River mouth. Sampling times and sites were outlined in more detail in Chapter 1. All sampling followed the protocol for 57 cm bongo oblique tows to 18.5 metres outlined in Chapter 2.

Concentrations for individual species, total species and eggs were analysed and data from the same months were pooled, $\sqrt{(x+1)}$ transformed and subjected to a 2-way ANOVA between months and stations, with the confidence level set at 95%. Tukey's multiple range test was applied to search for homogeneous groups and contrast.

RESULTS

Temporal Distribution

From a total of 219 bongo tows and 30 RMT1x6 hauls (48 403.05 m^3 of filtered water), a total of 11 327 fish larvae, 97 268 eggs and 29 squid para- larvae were sampled (Table 5.1). Of the total larvae, thirty-nine were unidentified or unidentifiable due to severe damage. Seventy-five taxa were

Table 5.1 - Checklist, concentrations and percentage composition of ichthyoplankton and squid para-larvae caught within the study area for the period between August 1993 and October 1996. Included are the months (year in parenthesis) during which each species was dominant at Middlebank and at all stations combined, as well as an indication of occurrence at Middlebank (M) and 5, 10 & 15 nautical miles along the offshore transect. [# denotes a species endemic to southern Africa according to Smith & Heemstra (1986), and * denotes those species illustrated and described in Chapter 4].

FAMILY	SMITH'S NUMBER	SPECIES	COMMON NAME	TOTAL NUMBER	Conc. (#/M^3)	%	Dominant Months		Presence at Transect Stns.
							Middlebank	All Stations	
Clupeidae	54.2	*Etrumeus whiteheadi*#	Redeye roundherring	487	0.01006	4.30	Ag('93);Jn('95);A('96)	Ag,N('93);O('95);A('96)	M, 5, 10
	54.12	*Sardinops sagax*	Pilchard	5614	0.11598	49.56	Ag('93);Ag-N('94); Jn-Ag('95);Jl('96)	Ag,N('93);Ag-N('94); Jn-Ag('95);Jl('96)	M, 5, 10, 15
Engraulidae	55.1	*Engraulis japonicus*	Cape anchovy	715	0.01477	6.31	My,N('94);J('95&'96)	N('93); J('95&'96)	M, 5, 10, 15
Gonorhynchidae	57.1	*Gonorhychus gonorhynchus*	Beaked sandfish	1	0.00002	0.01	N('94)		
Myctophidae	86.42	*Diogenichthys atlanticus*	Laternfish	2	0.00004	0.02		Ag('93);O('95)	
	86.72	*Lampanyctodes hectoris*	Onderbaadjie	33	0.00068	0.29		Jl('95)	5, 10
	86.119	*Symbolophorus barnardi*	Lanternfish	4	0.00008	0.04		O('95)	
	86.?	*Hygophum* sp.*	Lanternfish	2	0.00004	0.02		Jl,Ag('95)	5, 10
Gadidae	88.1	*Gaidropsarus capensis*#	Cape rockling	76	0.00157	0.67	Ag('93);Jl-Ag('95)	Ag('93);Jl-Ag('95)	M, 5, 10
Merlucciidae	89.4	*Merluccius capensis*	Shallow-water hake	79	0.00163	0.70	Ag('93);A('96)	Ag('93);O('95);A('96)	10
Moridae	90.7	*Physiculus capensis*#	Deepsea cod	3	0.00006	0.03		O('95)	
Bregmacerotidae	92.1	*Bregmaceros atlanticus*	Codlet	5	0.00010	0.04	M('94);A('96)	O('95);A('96)	
Ophidiidae	96.9	*Genypterus capensis*#	Kingklip	3	0.00006	0.03	Ag('93)	Ag('93);O('95);A('96)	
Lophiidae	101.4	*Lophius upsicephalus*	Monk	1	0.00002	0.01		O('95)	
Gobiesocidae	110.?	Species 1*	Clingfish	195	0.00403	1.72	Ag('94)	Ag,N('93);O('95)	
	110.?	Species 2*	Clingfish	21	0.00043	0.19	Ag('94);A('96)	Ag('93);O('95);A('96)	
	110.?	Species 3*	Clingfish	5	0.00010	0.04	A('96)	O('95);A('96)	
Zeidae	138.5	*Zeus faber*	John Dory	5	0.00010	0.04	Ag('93);Jn('95)	Ag('93);Jn('95);Jl('96)	M
Syngnathidae	145.29	*Syngnathus acus*	Longsnout pipefish	2	0.00004	0.02		Ag('95);A('96)	10
Tetrarogidae	150.2	*Coccotropsis gymnoderma*#	Smoothskin scorpionfish	33	0.00068	0.29	N('94)	N('93);F,Ag('95);My,O('96)	M, 5, 15
Congiopodidae	152.1	*Congiopodus spinifer*#	Spinenose horsefish	4	0.00008	0.04	A('96)	O('95);A('96)	
Triglidae	157.1	*Chelidonichthys capensis*#	Cape gurnard	96	0.00198	0.85	Ag('93);Jl('95)	Jl-O('95)	M, 5, 10

Table 5.1 continued.

FAMILY	SMITH'S NUMBER	SPECIES	COMMON NAME	TOTAL NUMBER	Conc. (#/M³)	%	Dominant Months		Presence at Transect Stns.
							Middlebank	All Stations	
Serranidae	166.76	*Serranus cabrilla*	Comber	1	0.00002	0.01	Ag('93)	Ag('93)	
Haemulidae	179.17	*Pomadasys olivaceum**	Grunter	20	0.00041	0.18	Ag('93)	Ag('93),Jl-Ag('95);M('96)	5, 10
Sparidae	183.5	*Argyrozona argyrozona#*	Carpenter	129	0.00267	1.14	Ag('93),Jn('95)	Ag('93)	M, 5, 10
	183.6	*Boopsoidea inornata*#*	Fransmadam	25	0.00052	0.22		O('95)	
	183.11	*Chrysoblephus laticeps#*	Roman	22	0.00045	0.19	Ag('93);O('96)	Ag('93);N('95)	5, 10
	183.16	*Diplodus cervinus hottentotus#*	Zebra	1	0.00002	0.01		N('95)	5
	183.17	*Diplodus sargus capensis*	Blacktail	117	0.00242	1.03	Ag('93)	Ag('93)	M, 5, 10
	183.25	*Pagellus bellotti natalensis*	Red tjor-tjor	26	0.00054	0.23	Jn-Jl('95)	Jl-Ag('95);M('96)	M, 5, 10, 15
	183.39	*Sarpa salpa*	Strepie	5	0.00010	0.04	My,Ag('94)	N('93);N('95)	10
	183.41	*Spondyllosoma emarginatum#*	Steentjie	21	0.00043	0.19	N('95)	N("93,'94,'95)	
	183.?	Species 3*	Seabream	5	0.00010	0.04	N('94)	Ag,N('93)	
	183.?	Species 6*	Seabream	9	0.00019	0.08	N('94);J('96)	A,O,N('95);J('96)	M, 5, 10
	183.?	Species 10*	Seabream	3	0.00006	0.03	A('96)	N('93);M-A('96)	10
	183.?	Species 11*	Seabream	334	0.00690	2.95	Jl('95)	Jl('95)	M, 5, 10
	183.?	Species 12*	Seabream	2	0.00004	0.02		Ag,N('95)	5
	183.?	Species 13 *	Seabream	1	0.00002	0.01	Jn('95	Jn('95)	M
Monodactylidae	193.2	*Monodactylus falciformis*	Cape moony	1	0.00002	0.01		F('95)	15
Sciaenidae	199.3	*Atractoscion aequidens*	Geelbek	4	0.00008	0.04		N('93,'95);M('96)	5, 10
	199.?	Species 1*	Kob	2	0.00004	0.02		F,Ag('95)	
	199.?	Species 2*	Kob	1	0.00002	0.01		O('95)	
Carangidae	210.44	*Seriola lalandi*	Giant yellowtail	1	0.00002	0.01	A('96)	A('96)	
	210.52	*Trachurus trachurus capensis*	Maasbanker	1749	0.03613	15.44	Ag('93);Jn('95)	Ag('93);Jl,Ag,O('95)	M, 5, 10
Cheilodactylidae	215.1	*Chellodactylus fasciatus#*	Redfingers	10	0.00021	0.09	Ag('93);Jl('95)	Ag('93);Jl,Ag('95)	M, 5
	215.3	*Chirodactylus brachydactylus#*	Twotone fingerfin	1	0.00002	0.01		N('94)	
	215.?	Species 1*	Fingerfin	65	0.00136	0.58	Ag('93);Jn('95)	Jl,Ag('95)	M, 5, 10
	215.?	Species 2*	Fingerfin	6	0.00012	0.05		Jn,Ag('95)	5, 10
Mugilidae	222.7	*Liza richardsonii#*	Southern mullet	2	0.00004	0.02		N('93,'95)	5
	222.10	*Mugil cephalus*	Flathead mullet	2	0.00004	0.02	N('94)		
	222.?	Species 3*	Mullet	1	0.00002	0.01	N('93);F('95)		15

Table 5.1 continued.

FAMILY	SMITH'S NUMBER	SPECIES	COMMON NAME	TOTAL NUMBER	Conc. (#/M^3)	%	Dominant Months: Middlebank	Dominant Months: All Stations	Presence at Transect Stns.
Champsodontidae	229.1	*Champsodon capensis*	Gaper	1	0.00002	0.01		O('95)	
Blenniidae	235.33	*Parablennius pilicornis*	Ringneck blenny	84	0.00174	0.74	Ag('93,'94);N('95)	Ag,N('93);F('95)	M, 5, 10, 15
	235.40	*Scartella emarginata*	Maned blenny	1	0.00002	0.01	M('94)	N('93)	
	235.?	Species 3*	Blenny	7	0.00014	0.06		Ag,N('93);O('95)	
	235.?	Species 4*	Blenny	46	0.00095	0.41	Ag,S('94)	N('93)	M, 15
	235.?	Species 5*	Blenny	18	0.00037	0.16	Ag('94);J('96)	N('93);F,O('95);J('96)	M, 10
	235.?	Species 6*	Blenny	3	0.00006	0.03	Jl('96)	Ag('95);Jl('96)	10
Ammodytidae	238.2	*Gymnammodytes capensis*'#	Cape sandlance	2	0.00004	0.02	J('96)	J,A('96)	M
Callionymidae	239.6	*Paracalllonymus costatus*#	Ladder dragonet	429	0.00886	3.79	Ag('93);A('96)	N('93);A('96)	M, 5, 10
Gobiidae	240.?	Species 1*	Goby	88	0.00182	0.78	Ag('95)	Ag,O('95)	M, 10
	240.?	Species 2*	Goby	68	0.00140	0.60	My('94);A,Jl('96)	Ag('93);O('95);A,Jl('96)	
	240.?	Species 3*	Goby	23	0.00048	0.20	Ag('94);A('96)	Jn,Ag,O('95);A('96)	10
	240.?	Species 4*	Goby	1	0.00002	0.01		Ag('93)	
Gempylidae	247.8	*Thyrsites atun*	Snoek	23	0.00048	0.20	Ag('93)	Ag('93);Jl('95)	10
Trichiuridae	248.4	*Lepidopus caudatus*	Buttersnoek	10	0.00021	0.09	O('95)	A,Ag('95)	10
Scombridae	249.11	*Scomber japonicus*	Mackerel	31	0.00064	0.27	Ag('93)	Ag,O('95)	
Bothidae	259.1	*Amoglossus capensis*#	Cape flounder	1	0.00002	0.01		Ag('95)	5
Cynoglossidae	261.3	*Cynoglossus capensis*#	Sand tonguefish	6	0.00012	0.05	A('96)	Jl,Ag,O("95);A('96)	5
	261.9	*Cynoglossus zanzibarensis**	Redspotted tonguefish	339	0.00700	2.99	N('94);A('95)	N('93);O('95)	M, 5, 10, 15
Soleidae	262.3	*Austroglossus pectoralis*'#	East coast sole	131	0.00271	1.16	N('94)	N('93)	M, 5, 10
	262.5	*Heteromycteris capensis*#	Cape sole	18	0.00037	0.16	S('94);F('96)	O('95);A('96)	M, 10
	262.7	*Monochirus ocellatus*	Foureye sole	3	0.00006	0.03	A('96)	A('96)	
	262.12	*Solea bleekeri*#	Blackhand sole	1	0.00002	0.01	M('96)	M('96)	M
	262.15	*Synaptirichthys kleini*	Lace sole	2	0.00004	0.02	A('95)	A,O('95)	M
		Total larvae		11327	0.23420	100.00			
		Total Eggs		97268	2.00954				
		***E. japonicus* eggs**		5073	0.10481	5.22			
Loliginidae		*Loligo vulgaris reynaudii*	Chokka squid	29	0.00060		A('96)	Ag('93);O('95);A('96)	

identified to either family, genus or species level. Of these, the four most abundant species were pelagics important to the commercial trawl fishery. The most dominant was *S. sagax*, comprising 49.6% of the total catch, followed by *T. t. capensis* at 15.4%, although the majority of these came from extremely high catches in the August 1993 samples. The next most prolific species were *E. japonicus* and *E. whiteheadi* which made up 6.3% and 4.3% of the overall catch respectively. The only other species to make up more than 1% of the catch were Gobiesocidae Species 1 (1.72%), *A. argyrozona* (1.14%), *D. s. capensis* (1.03%), Sparidae Species 11 (2.95%), *P. costatus* (3.79%), *C. zanzibarensis* (2.99%) and *A. pectoralis* (1.16%). The majority of Sparidae Species 11 and Gobiesocidae Species 1 were caught in samples from July 1995 and August 1993 respectively. With the removal of the dominant *S. sagax*, several other species such as *Gaidropsarus capensis* (1.33%), *M. capensis* (1.38%), *Chelidonichthys capensis* (1.68%), Cheilodactylidae Species 1 (1.15%), *P. pilicornis* (1.47%) and Gobiidae Species 1 and Species 2 (1.54% & 1.19%) contributed reasonably to the total. Forty-nine fish species and the squid para-larvae were present infrequently and in low concentrations (Appendix 11), and as such were precluded from any statistical analysis.

In a previous survey of the ichthyoplankton assemblage in the TNP (Tilney & Buxton 1994) between January 1991 and July 1992, 24 families were represented by their early life history stages as opposed to 35 in this study. While the Tetraodontidae were represented by three *Amblyrhynchotes honckenii* specimens, and three unidentified species of clinids were encountered in the previous survey, none were encountered here. All the other families identified by Tilney & Buxton (*op. cit.*) were again encountered, and the 13 families which were not present in their samples but which were identified during the course of this study appear in Table 5.2. Of these, four were represented by single specimens, namely Gonorrhynchidae, Lophiidae, Champsodontidae and Bothidae. Some of the new family additions to the ichthyoplankton checklist were well represented. The 41 myctophids comprised mainly *L. hectoris* (33), but also included *Diogenichthys atlanticus* (2), *Symbolophorus barnardi* (4) and *Hygophum* sp. (2). All 79 merlucciids were *M. capensis*, the 23 gempylids were all *Thyrsites atun*, and *Scomber japonicus* made up the total (31) for the scombrids.

Spatial Distribution

A total of 1 595 larvae and 49 601 eggs were collected from 16 509.65 m^3 of water. Forty-nine species from 24 families were identified, 17 of which (Appendix 12) were present in sufficient numbers for further analysis. The remaining 32 species which did not occur frequently enough or in sufficient concentrations for statistical analysis are presented in Appendix 13.

Table 5.2 - New additions to the ichthyoplankton checklist for the south-east Cape. Only those taxa which could be identified to species level are included here, e.g. Sparidae Species 3 was not considered.

FAMILY	SPECIES	NUMBER
Gonorhyichidae	*Gonorhynchus gonorhynchus*	1
Myctophidae	*Diogenichthys atlanticus*	2
	Lampanyctodes hectoris	33
	Symbolophorus barnardi	4
	Hygophum sp.	2
Merluccilidae	*Merluccius capensis*	79
Moridae	*Physiculus capensis*	3
Bregmacerotidae	*Bregmaceros atlanticus*	5
Ophidiidae	*Genypterus capensis*	3
Lophiidae	*Lophius upsicephalus*	1
Zeidae	*Zeus faber*	5
Gempylidae	*Thyrsites atun*	23
Champsodontidae	*Champsodon capensis*	1
Trichiuridae	*Lepidopus caudatus*	10
Scombridae	*Scomber japonicus*	31
Bothidae	*Arnoglossus capensis*	1

Using a similar classification to Tilney & Buxton (1994), where larvae were grouped according to the habitat most frequently occupied by the adults, there were representatives from all three groups of pelagic-, sand- and reef-associated larvae, although the classification was not this simple in some cases. Amongst the pelagic component was *Hygophum* sp. and *T. atun*. The sand-associated fauna included *M. capensis*, *Zeus faber*, *Syngnathus acus*, *Liza richardsonii*, Mugilidae Species 3, *Gymnammodytes capensis*, *Cynoglossus capensis*, *Heteromycteris capensis*, *Solea bleekeri*, *Synapturichthys kleini* and *Arnoglossus capensis*. Larval species whose adults are reef dwellers incorporated *Diplodus cervinus hottentotus*,

Sarpa salpa, Sparidae Species 6, 10, 12 and 13, *Monodactylus falciformis*, *Pomadasys olivaceum*, *Cheilodactylus fasciatus*, Cheilodactylidae Species 1 and 2, Blenniidae Species 4, 5 and 6, and Gobiidae Species 1 and 3. Based on the description of the adult habitat, certain species could not be classified into any one group, for example *Scomber japonicus* is described as both epipelagic and demersal (Collette 1986), and *Lepidopus caudatus* is benthopelagic (Nakamura 1986). Furthermore it is assumed that the unidentified sparids are reef-associated even though there are some within the family, e.g. *Pagellus bellotti natalensis* which are known to be sand-associated. Likewise, *Atractoscion aequidens* can be found in a wide range of habitats, and the two unidentified sciaenid species could be sand- or reef-associated. Despite the low concentrations it is interesting to note that larvae from a number of the reef-associated species were found at offshore (≥ 5 nm) stations where no reef was recorded on the echo-sounder trace. In addition, species such as *Z. faber*, *Gymnammodytes capensis*, *Cynoglossus capensis*, *H. capensis*, *S. bleekeri* and *S. kleini* were found over the reef area of Middlebank which shows that their larvae are not necessarily retained over sand substrates where they are spawned.

For those species of larvae and eggs which featured more prominently in the monthly and offshore transect catches, the following was observed:

Total Larval Concentrations

Temporal - Of the 11 327 larvae which were caught, 7 426 came from the 15 samples in August 1993 making this the most productive month (Figure 5.1) with concentrations of 4.08/m^3 (5 460 larvae) for Middlebank and 1.94/m^3 for all stations combined. Larval concentrations never attained those levels again but concentrations > 0.11/m^3 were obtained on Middlebank for November 1994 and in June and July 1995 (Figure 5.1), while the period July to October 1995 consistently produced catches in excess of 0.25/m^3, peaking at 0.6/m^3, for all stations combined. The lowest concentration of larvae caught from Middlebank was 8.65E-5/m^3 in May 1996, with the lowest overall concentration for all stations being 0.0014/m^3 in March 1995. The months of February and March consistently produced the lowest overall concentrations of larvae (Figure 5.1), a pattern also observed by Tilney & Buxton (1994) for the same months in 1992. This was explained by the impact of upwelling events whose drastic temperature variations resulted in high larval mortality. Catches of eggs during February and March were mostly higher than average (see

below) which helps illustrate that spawning was taking place, enforcing the idea that larval mortalities were high.

Spatial - The months of February, March and May were not particularly productive in terms of fish larvae, while January and August 1995 provided the maximum concentrations (Figure 5.2). In February 1995 only the 15 nm station and one site at 10 nm were sampled before the towing rope parted and the entire bongo array was lost. The low concentrations for this month were most likely as a result of this limited sampling. In March 1995 extremely dense aggregations of salps (Class: Thaliacea) at 5, 10 and 15 nm caused excessive net clogging. No larvae were caught, perhaps due to avoidance of the dense salp concentrations or due to backflushing resulting from the clogged mesh. These salps were also in evidence at Middlebank, but not in the same densities, and a few larvae were caught. A similar trend was observed with the eggs (see below). In February 1996 sea surface temperatures (SST's) were 14°C, 13°C and 12°C at 10 nm, 5 nm and Middlebank respectively. These cool surface waters are indicative of upwelling conditions which are known to affect larval survival and hence catches. Similarly in March 1996 the SST was 12°C at Middlebank, and no larvae were recorded, but further offshore at 5 and 10 nm, where the cold upwelled water had not yet penetrated, SST's were 15°C and 17°C respectively, and a few larvae were encountered. The bad catches in May 1996 were not accompanied by abnormally low temperatures (SST's were a uniform 16°C at all stations) and could have been an anomaly arising from extreme larval patchiness that month. The high larval concentrations in August 1995 were also accompanied by a uniform 16°C SST and a light five knot SW wind, i.e. similar conditions, different result. The good catches in January 1995 took place under conditions which appeared ideal for egg and larval survival. The SST ranged from 19.8°C at 15 nm to 19°C on Middlebank with a calm sea (± 3 foot swell) and a light (< 5 knot) WSW wind.

The results of the Kruskal-Wallis single factor ANOVA and the 2-way ANOVA revealed that there was no significant difference for total larval concentrations between seasons or between offshore transect stations respectively.

Total Egg Concentrations

Temporal - A total of 97 268 fish eggs were sampled during the study. 5 073 of which belonged to *E. japonicus* (caught during the October 1995 R.S. *Africana* voyage). These eggs will

be discussed later together with the larval distribution of the species. Egg concentrations were for the most part > 1.0/m^3 of water sampled (Figure 5.3). The most productive months for eggs on Middlebank were August 1993 and February 1996 when as many as 6.9/m^3 and 5.6/m^3 were caught. Overall, it was February 1995 with 5.3/m^3 which displayed the highest catches, although October 1995 to January 1996 produced consistently high catches between 4.7 and 5.0/m^3 (Figure 5.3). There were, however, times when concentrations were low (< 0.5/m^3) for Middlebank, during the months of May, August and November 1994, April 1995 and July 1996. For all the stations combined, the lowest concentrations (< 1.0/m^3) were recorded during March 1995 and May and July 1996.

Spatial - Catches along the transect between January 1995 and May 1996 were generally good. Even during cold water periods when larval densities were low, egg concentrations were still high (Figure 5.4). Interestingly, eggs, like fish larvae, were absent from offshore catches in March 1995 when the dense salp aggregations were encountered. Reduced water acceptance, backflushing and bad filtration efficiency in the gear could all have led to this phenomenon, as high concentrations (± 3.5/m^3) were encountered over Middlebank where salps were less concentrated.

As was the case for total larval concentrations, no significant differences were detected between seasonal or transect station egg concentrations.

Individual Species

Redeye roundherring (*Etrumeus whiteheadi*) - Peaks in abundance for Middlebank catches were August 1993, June 1995 and April 1996, while August and November 1993, October 1995 and April 1996 registered the greatest concentrations for all stations combined (Table 5.1). A total of 487 larvae were caught between August 1993 and October 1996. The concentrations on Middlebank were generally low, registering a maximum of just below 0.02/m^3 compared to maximum values ranging from 0.03 to 0.08/m^3 for combined stations (Appendix 14). The mean size and size range of larvae caught indicated most specimens were near to and undergoing flexion (Appendix 15). A few yolk-sac stage larvae (3.0 mm BL) were encountered, with the largest larva measuring 21.0 mm BL.

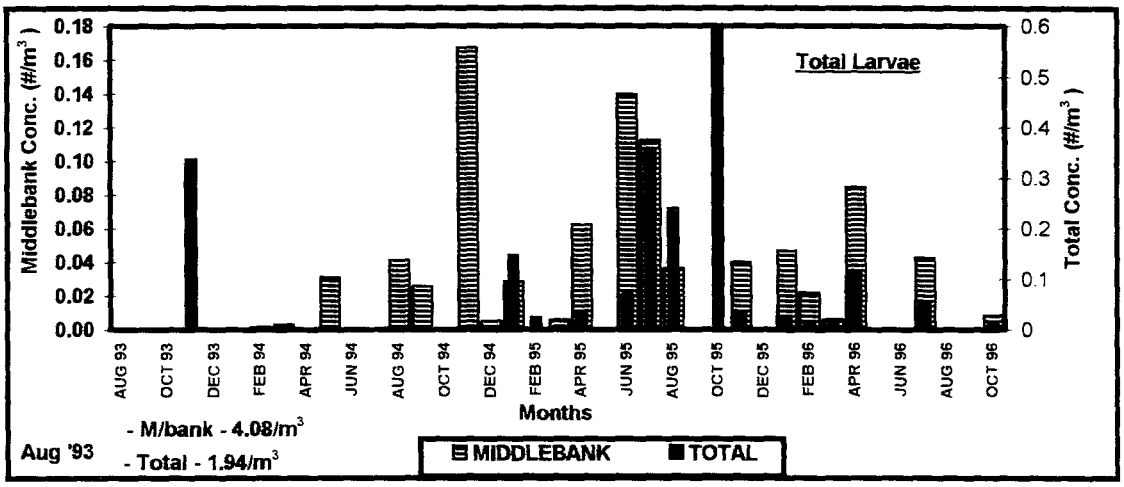


Figure 5.1 - Total concentrations of all fish larvae combined (larvae/m³) from Middlebank and for all stations combined (total) for each month from August 1993 to October 1996. The concentrations for August 1993 appear in the lower left corner as a result of them being an order of magnitude higher than any others.

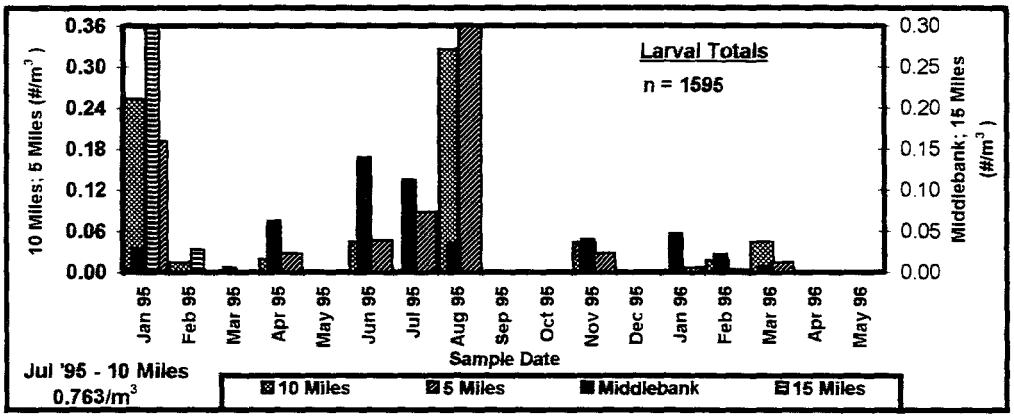


Figure 5.2 - Total concentrations (larvae/m³) of all fish larvae combined from the 5, 10 & 15 miles sites off Storms River and from Middlebank for each month from January 1995 to May 1996. The high concentration at 10 miles during July 1995 appears in the lower left corner to accommodate the axis scales for the rest.

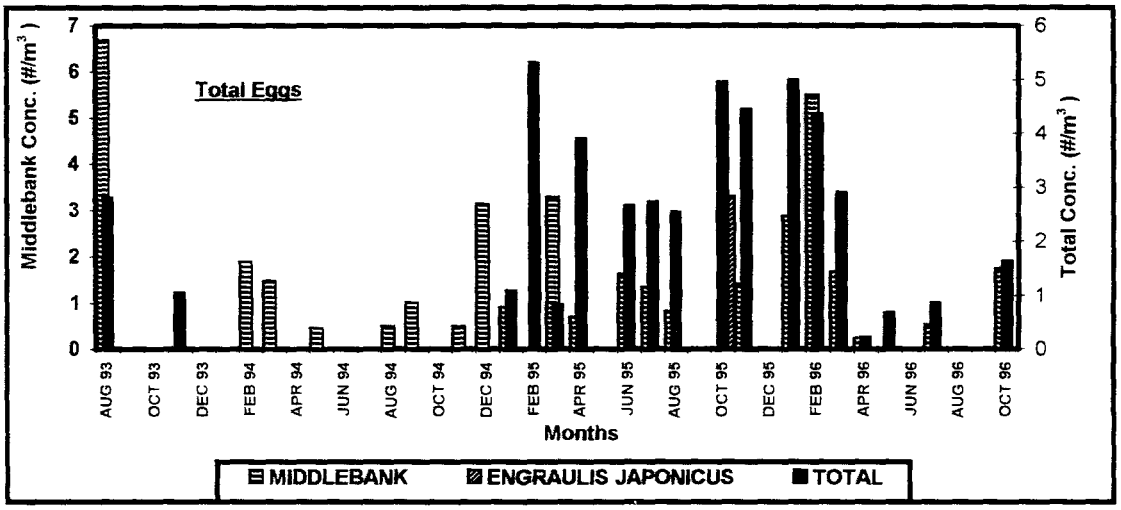


Figure 5.3 - Total concentration of fish eggs (eggs/m³) from Middlebank and for all stations combined (total) for each month from August 1993 to October 1996.

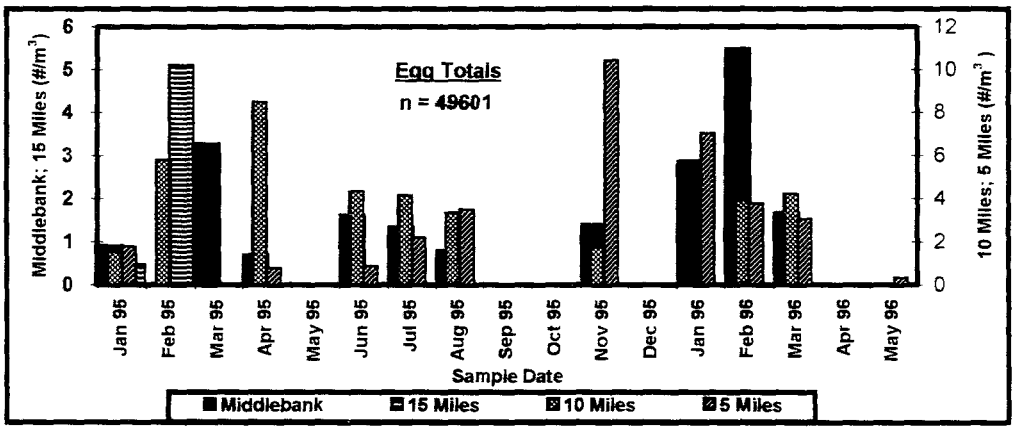


Figure 5.4 - Total concentration of fish eggs (eggs/m³) from the 5, 10 & 15 miles sites off Storms River and from Middlebank for each month from January 1995 to May 1996.

No *E. whiteheadi* larvae were found out at 15 nm, and apart from June 1995 when larvae were found at Middlebank and five nm, their distribution appeared patchy, being caught at single stations each month (Appendix 12). No statistical difference was observed for larval concentrations between stations, although the low overall catch (n = 8) should be taken into account when interpreting these results.

Pilchard (*Sardinops sagax*) - By far the most prolific of the larvae caught, with 5 614 found in samples from 19 months. Peaks in abundance were evident during August 1993, August and November 1994, June to August 1995, and July 1996 over Middlebank (Table 5.1). For all stations combined, August 1993, and August and October 1995 provided the highest concentrations. Apart from August 1993, when exceptionally high concentrations were caught, concentrations ranged between 0.005 and 0.05/m^3 for Middlebank and 0.003 and 0.12/m^3 for combined sites (Appendix 14). Size at hatching for *S. sagax* is small, with yolk-sac specimens around the 2.0 mm BL class being captured (Appendix 15). However, the mean sizes indicate that these small individuals were uncommon, probably as a result of being undersampled with the larger 505 µ mesh nets. Although there were many larvae undergoing flexion, there was an absence of any large postflexion larvae over 22.4 mm BL. The large range of sizes present in most samples (Appendix 15) indicates an active retention of larvae within the sampling area, at least until a threshold size (> 23.0 mm BL) is attained at which time it appears that they avoid capture by the net.

A total of 431 *S. sagax* larvae were found at all stations along the transect, although only once in low concentration (0.0019/m^3) at 15 nm in February 1995 (Appendix 12). During the winter/spring spawning peak there appeared to be more larvae on Middlebank and at 10 nm, with only a single peak at five nm in August 1995 (Appendix 12). Overall, however, statistical analysis showed that larvae were evenly distributed along the offshore transect.

Cape anchovy (*Engraulis japonicus*) - A total of 715 larvae were present in catches from 19 out of 25 months, with maximum concentrations at Middlebank coming from May and November 1994, January 1995, and January 1996. Larvae from all other stations were most prevalent in November 1993, January 1995, and January 1996 (Table 5.1; Appendix 14). The presence of only a few eggs in the August 1995 samples may have indicated the start of a spawning event as no larvae were present. By October 1995 as many as 3.4 eggs/m^3 were being sampled (Figure 5.3). The mean size of larvae (Table 5.8) show that the majority of fish caught were < 10 mm BL, just

above the size at flexion of 8.7 mm BL, with the smallest individual being a 1.8 mm BL yolk-sac larva (Appendix 15). Movement in small preflexion individuals is restricted, making avoidance difficult, and their elongated bodies decrease the chances of escapement or extrusion through the mesh. Larger flexion and postflexion larvae were also frequently caught, with the largest individual measuring 31.86 mm BL (Appendix 15).

This species was the third most abundant along the offshore transect stations (n = 292). Larvae were found at all four stations along the transect in January 1995, but subsequent to this they were only found at 10 nm and Middlebank (Table 5.1). The high concentrations at all stations in January 1995 (Appendix 12) ensured that overall there was no significant difference between distributions.

Onderbaadjie (*Lampanyctodes hectoris*) - Larvae were absent from Middlebank, and only appeared in samples when the 5 and 10 nm stations off Storms River mouth were sampled. Their presence in samples from seven months amounted to 33 individuals (Table 5.1) with catches from April 1995, March 1996, and July 1996 consisting of single individuals. The only real significant catch was in July 1995 when a concentration of 0.013/m^3 (22 animals) was recorded (Appendix 14). The size range of this catch incorporated both preflexion and flexion individuals (Appendix 15), with a mean size of just below 6.0 mm BL.

The overall absence of these larvae in summer (see above) is the most feasible explanation for their absence from the 15 nm stations which were only sampled in the summer months. No larvae were encountered over the inshore station of Middlebank either, and although only encountered at 5 and 10 nm (Table 5.1; Appendix 12), the low number of specimens caught (30) meant that a significant difference could not be detected between stations.

Cape rockling (*Gaidropsarus capensis*) - Larvae were caught frequently during the program with the exception of summer months. Concentrations were generally on the low side, with notable catches only coming from August 1993, July 1995, and August 1995 at Middlebank and for all stations combined (Table 5.1; Appendix 14). Size at hatching must be small as yolk-sac larvae of 1.3 and 1.4 mm BL were caught. Larvae as large as 21.4 mm BL which had undergone complete flexion were also caught (Appendix 15), reflecting the susceptibility of all size ranges of this species to the gear. Flexion was evident already in all three larvae above 5.6 mm BL. The small mean size of < 5 mm BL (Appendix 15) which characterised most catches may be indicative of patchy

spawning or movement away from the spawning area by flexion larvae once their swimming abilities increase.

This species was found at all sites except 15 nm (Table 5.1), with the 35 larvae captured being distributed evenly in low concentrations amongst the other three sites (Appendix 12) such that no significant difference was detected.

Shallow-water hake (*Merluccius capensis*) - Samples from eight months produced 79 hake larvae ranging in size from 1.6 mm BL to 15.7 mm BL (Appendix 15). Four months were represented by single individuals, and the highest concentrations were in August 1993 and April 1996 for both Middlebank and all stations, and October 1995 for all stations only (Table 5.1; Appendix 14). Mean sizes were variable with catches of more than one larva coming from four different months. The presence of flexion larvae, > 7.0 mm BL, and in particular the size range in the April 1996 catch (Appendix 15) suggests retention in the sampling area on at least one occasion.

Gobiesocidae Species 1 - A total of 195 larvae were caught, with the majority of those (175) coming from inshore stations at Steilkop and Rheeders in August 1993. Their appearance in samples was sporadic, only being found in samples in the months of August, October and November (Table 5.1; Appendix 14). The mean sizes (Appendix 15) illustrate the paucity of animals < 3.0 mm BL and > 5.0 mm BL.

Gobiesocidae Species 2 - A total of only 21 larvae were caught from four months, with the highest concentration coming from August 1993 (Table 5.1). The absence of both this species and Gobiesocidae Species 1 from Middlebank during August 1993 (Appendix 14) and low concentrations for both subsequent to this from sample sites further offshore may be indicative of a preference for inshore spawning and retention of larvae. The mean sizes (Appendix 15) are larger than for the previous species.

Smoothskin scorpionfish (*Coccotropsis gymnoderma*) - These larvae appeared frequently in catches, although never in any great numbers, with the greatest concentrations coming from Middlebank in November 1994 and all stations in November 1993 (Table 5.1; Appendix 14). Caudal flexion was evident in larvae > 4.6 mm BL, with the largest individual collected (5.8 mm

BL - Appendix 15) not yet displaying postflexion characteristics. The trend of low concentrations make assumptions difficult, but the size ranges of those caught during November 1993 and March 1994 indicate prolonged spawning and retention of larvae. A mean size of above 4.0 mm BL for the most part (Appendix 15) indicates either a distribution pattern for smaller individuals which excluded the sampling range of the gear or an ability to escape through the mesh. Large postflexion animals were also absent, perhaps signalling an early settlement behaviour for this highly cryptic benthic species.

Cape gurnard (*Chelidonichthys capensis*) - Present frequently in samples with highest concentrations coming during August 1993 and the period July - October 1995 (Table 5.1). The highest concentration of 0.025/m^3 was caught far from Middlebank, whose biggest contribution was 0.006/m^3 in August 1993 (Appendix 14). A large size range at times and large variation in the mean sizes (Appendix 15) indicated a protracted spawning habit for adult fish, retention of all early stages in the sampling area, and a susceptibility of most stages to the sampling gear. Individuals measuring 1.8 and 2.0 mm BL were still in the yolk-sac stage, while those > 6.4 mm BL all exhibited notochord flexion. Fin development in larvae > 8.0 mm BL was advanced, with all remnants of the finfold gone and only the caudal fin showing a lack of its full complement of elements.

A total of 70 larvae were caught at all stations from the transect line, except at 15 nm (Table 5.1). As a result of mostly low concentrations, no significant difference between stations could be found, despite the relatively high concentrations during July and August 1995 (Appendix 12).

Olive rock grunter (*Pomadasys olivaceum*) - Only 20 larvae were caught during the study with greatest concentrations in August 1993 and August 1995 at Middlebank, and in August 1993, July - August 1995 and March 1996 at all stations combined (Table 5.1; Appendix 14). The size range of larvae, particularly in July and August 1995 (Appendix 15), contained individuals in stages of early preflexion as well as late flexion. The majority of larvae, indicated by their mean sizes were undergoing flexion, showing that the gear or sampling regime was ineffective in attaining a representative sample of the smaller preflexion fish. The larger larvae between 8.3 and 9.4 mm BL were late flexion with fin elements prominent but not yet fully developed.

Carpenter (*Argyrozona argyrozona*) - Present in low concentrations from ten months, except for August 1993 and June 1995 at Middlebank, and August 1993 overall when good catches were made (Table 5.1; Appendix 14). The smallest individual captured was a yolk-sac 1.8 mm BL larva. The majority of larvae were preflexion animals between 3.0 and 4.0 mm BL (Appendix 15), with notochord flexion evident in larvae > 4.3 mm BL. The largest larvae between 4.5 and 4.8 mm BL were all still in the early flexion stage. Larger larvae had either moved away from the sample areas prior to late flexion and postflexion development, or had evaded capture, although other sparid species larger than this were frequently caught during the study.

Argyrozona argyrozona larvae were present in small concentrations, mainly at Middlebank and the five nm stations (Appendix 12). They were absent at 15 nm and occurred only once at 10 nm (Table 5.1). No significant difference could, however, be detected between stations, most likely as a result of their apparent diffuse distribution leading to poor catches.

Roman (*Chrysoblephus laticeps*) - Concentrations were generally low, with a total of only 22 animals being caught. Highest concentrations over Middlebank were evident during August 1993 and October 1996, with most larvae from combined stations in August 1993 and November 1995 catches (Table 5.1; Appendix 14). The smallest individual captured was a preflexion 2.6 mm BL larva with no evidence of a yolk-sac, and the largest animal sampled was a 7.8 mm BL postflexion larva. Larvae of 5.3 mm BL were still in the preflexion condition, but notochordal flexion had started by 5.6 mm BL. While the overall size range caught showed their susceptibility to the bongo gear, catches comprising more than one individual did not encompass any substantial size ranges (Appendix 15).

Only six *C. laticeps* larvae were identified from the plankton samples along the transect, and all were caught either at five or ten nm (Table 5.1; Appendix 12) although specimens were collected on Middlebank prior to January 1995 and after May 1996. The paucity of larvae once again was likely the reason for the lack of a significant difference between sites.

Blacktail (*Diplodus sargus capensis*) - A total of 117 larvae were caught, with the majority coming from August 1993 (Table 5.1) with concentrations from Middlebank and other stations both registering over 0.02/m^3 (Appendix 14). The smallest larva was still in the yolk-sac stage and measured only 1.8 mm BL. With the exception of June 1995 mean sizes were all below 4 mm BL (Appendix 15). All larvae caught were preflexion, with even the largest specimen (7.4 mm BL) not

showing any sign of notochordal flexion. The wide size range represented in catches where substantial numbers were caught (Appendix 15) probably reflects a degree of retention with the larger preflexion and flexion larvae avoiding capture.

The period from June to August 1995 was the most productive along the transect (Appendix 12) with larvae being found at Middlebank and offshore at the five and ten nm stations (Table 5.1). None were found at 15 nm during the study. As only 21 larvae were caught in samples from five months, no significant trend in offshore distribution could be detected.

Red tjor-tjor (*Pagellus bellotti natalensis*) - Only 26 were present in samples from eight months. Highest concentrations were observed for the period June - July 1995 at Middlebank, and July - August 1995, and March 1996 at all stations (Table 5.1; Appendix 14). Many of the catches included a wide size range of larvae (e.g. July 1995 - Appendix 15) which included both preflexion and flexion larvae, suggesting the retention of most developmental stages in the same area. Larvae measuring 5.3 mm BL were still present in the preflexion state, but all those >5.6 mm BL represented the flexion condition. Stages missing from the samples included yolk-sac stages and early preflexion larvae, with the smallest larvae represented measuring 3.5 mm BL.

A small number of *P. b. natalensis* larvae (n = 21) were caught frequently, in samples along the transect from six out of twelve months, with the winter months from June to August 1995 producing the most specimens (Appendix 12). Larvae were found at all four stations (Table 5.1) and their distribution along the transect was found to be homogeneous.

Steentjie (*Spondyliosoma emarginatum*) - Larvae were present on only three occasions and in low concentrations (Appendix 14), but all were caught during the months of November (Table 5.1). The mean larval size was greater than 4.0 mm BL, but substantial deviations reflect the large size range present, particularly in samples from 1994 and 1995 (Appendix 15), with the sample with the largest size range coinciding with the highest concentration. The smallest larva sampled was 2.4 mm BL and had no evidence of a yolk-sac. Flexion was recorded at around 6.2 mm BL.

Sparidae Species 11 - Although 334 larvae of this species were caught, the majority of these (322) came from the samples in July 1995 (Table 5.1; Appendix 14). Both the size range and mean sizes indicate that the majority of larvae were preflexion with few < 3.0 mm BL (Appendix 15).

The size range of larvae caught in July 1995 is misleading as most were between 3.0 mm and 4.0 mm BL, but the presence of larger and smaller larvae does point to a certain degree of retention of the middle order size classes within the sample area.

Due to an exceptionally large catch in July 1995 (Appendix 12), this species was the second most abundant in catches along the transect in terms of numbers (n = 331), after the pilchard. Although no larvae were found at the 15 nm station (Table 5.1), overall concentrations between sites were not significantly different.

Maasbanker (*Trachurus trachurus capensis*) - The maasbanker provided the second most larvae totalling 1 749 from eight months, with the highest concentrations coming from August 1993 when 1 588 were captured (Table 5.1; Appendix 14). Compared to this, the rest of the samples looked meagre, although reasonable concentrations were caught in June 1995 at Middlebank, and during July, August and October 1995 from combined stations. The smallest larvae measuring 1.7 mm BL still had the remnants of a yolk-sac, but this had disappeared by the 2.2 mm BL stage. All larvae greater than 5.7 mm BL exhibited flexion, while those > 10.0 mm BL were considered postflexion with a full complement of fin elements even though they were not necessarily completely ossified. The majority of larvae were below 5.0 mm BL, but there were indications of extreme size ranges, e.g. 2.7 - 10.5 mm BL in August 1995 (Appendix 15), which point to prolonged spawning habits in a restricted area followed by retention of most early stages.

In accordance with the winter spawning peak registered above, the largest proportion of the 78 maasbanker larvae caught along the transect came from June - August 1995 (Appendix 12). Once again, larvae of this species were not caught at the 15 nm station, but were present at all other sites (Table 5.1). No significant difference could be found for concentrations between stations.

Cheilodactylidae Species 1 - A total of 66 larvae were caught, the majority of which came during August 1993 and June 1995 at Middlebank, and July and August 1995 from combined sites (Table 5.1). Concentrations on Middlebank were low, with the bulk of the numbers being made up from other stations (Appendix 14). The mean size of larvae was, with the exception of the single November 1994 specimen, < 5.0 mm BL (Appendix 15). None of the larvae had attained the flexion stage. A single larva was caught at night during routine bongo samples in November 1994 from the R.S. *Algoa* and was classed as a large postflexion paper-larva which was laterally

compressed and without the characteristic elongate pectoral fin rays. Nevertheless, fin elements were visible and the counts were that of *C. brachydactylus*. The difference in size between this larva and the remainder of the Cheilodactylidae Species 1 meant that no direct link could be made.

The 51 larvae which were identified from the transect stations were all found between April and August 1995 at five and ten nm as well as over Middlebank (Table 5.14; Appendix 12). Larvae were not recorded from 15 nm. Statistically, however, no stations along the offshore line produced significantly more larvae than another.

Ringneck blenny (*Parablennius pilicornis*) - This was by far the most abundant representative of the Blenniidae, totalling 84 larvae from 16 months. Although they appeared frequently in catches their concentrations were on the low side, with a high for Middlebank in August 1993, August 1994 and November 1995, and for combined stations in August and November 1993, and February 1995 (Table 5.1; Appendix 14). The smallest larvae in these samples, between 1.9 and 2.8 mm BL, were devoid of yolk-sacs. All larvae > 5.5 mm BL showed evidence of notochord flexion. The size ranges in catches (Appendix 15) showed that larvae became susceptible to the gear soon after hatching and that most stages could be found congregated together. The larger larvae caught (> 8.0 mm BL) were not yet postflexion. The majority of larvae were < 5.0 mm BL still with the finfold intact and little evidence of fin development, with the exception of the pectorals which begin development early on.

In this study, only 26 larvae were caught in samples from all four transect sites (Table 5.1; Appendix 12) mostly during winter and spring months. Low concentrations overall made interpretation difficult, but there appeared to be no significant difference between stations.

Blenniidae Species 4 - 46 larvae were caught in samples from eight months, with a peak for all stations combined in November 1993, and from August to September 1994 for Middlebank (Table 5.1; Appendix 14). No recently hatched larvae were caught, and the mean sizes (Appendix 15) reflect that most were preflexion. The largest larva (8.5 mm BL) was still regarded as undergoing flexion.

Blenniidae Species 5 - Although only 18 larvae were caught, they were present on nine occasions, being best represented in August 1994 and January 1996 at Middlebank, and October 1995 and January 1996 from combined stations (Table 5.1; Appendix 14). Only a few early flexion

larvae were caught and the mean sizes reflected this, with all values being < 4.0 mm BL (Appendix 15). Yolk-sac absorption was already complete even amongst the smallest (2.1 - 2.3 mm BL) larvae caught.

Ladder dragonet (*Paracallionymus costatus*) - The fifth most abundant type, totalling 429 individuals from 13 months. Highest concentrations came from samples during August 1993 and April 1996 at Middlebank, and November 1993 and April 1996 from combined stations (Table 5.1; Appendix 14). Many of the small specimens had been damaged by the net and could not be measured. Larvae < 1.5 mm BL possessed yolk-sacs. The extremely long notochord and the bent attitude which characterised most fixed larvae made the accurate detection of the onset of flexion difficult, but it appears that it is initiated at around 5.2 mm BL, with larvae > 8.0 mm BL being regarded as postflexion. The majority of larvae were preflexion, but many samples did include a large variety of sizes ranging from recently hatched to postflexion (Appendix 15). The samples in April 1996, obtained using the RMT on board the R.S. *Africana*, contained a high percentage of postflexion larvae in the night time samples resulting in a high mean size for that month (> 11.0 mm BL - Appendix 15).

A total of 23 dragonet specimens were caught from all sites except those at 15 nm at most times of the year (Table 5.1; Appendix 12) with no single month proving to be dominant. Even though larvae were only encountered on one occasion at five nm, concentrations were found to be homogeneously distributed across the spectrum of stations.

Gobiidae Species 1 - The most abundant of the goby species and also the most frequently caught, with the greatest concentrations in August 1995 at Middlebank, and August and October 1995 for combined stations (Table 5.1; Appendix 14). The mean sizes of captured larvae indicate that most larvae were preflexion animals (Appendix 15). No late stage postflexion larvae were observed.

Redspotted tonguefish (*Cynoglossus zanzibarensis*) - The most abundant and frequently caught pleuronectiform larvae, totalling 339 from 14 months. The most productive months were November 1994 and April 1995 for Middlebank, and November 1993 and October 1995 for all stations combined (Table 5.1; Appendix 14). The mean sizes indicated that most larvae were < 7.0

mm BL and therefore in the late preflexion to early flexion stages. Nevertheless, catches often comprised representatives from a wide range of sizes and developmental stages (Appendix 15).

Larvae were caught from all four transect sites, but only once at 15 nm, with the highest concentrations from the five nm and Middlebank samples in April 1995 (Table 5.1; Appendix 12). The 37 larvae caught were evenly distributed between the stations with no detectable significant difference in concentrations.

East coast sole (*Austroglossus pectoralis*) - 131 larvae of this species were caught in samples from 11 months, with highest concentrations for Middlebank and all other stations in November 1994 and November 1993 respectively (Table 5.1; Appendix 14). The majority of larvae caught were between 3.0 and 4.0 mm BL although large deviations at times, e.g. November 1993 (Appendix 15), were indicative of a wide range of developmental stages congregating together. No late flexion and postflexion larvae were caught in the samples.

A small number (n = 18) of these larvae were caught over Middlebank and at five and ten nm at some time during each of the seasons (Table 5.1). None were captured at the 15 nm site offshore. Due to the small number caught in five separate months, concentrations were low (Appendix 12) and significant differences could not be detected between stations.

Cape sole (*Heteromycteris capensis*) - Although this species occurred on a regular basis, concentrations were low with the more productive months being September 1994 and February 1996 at Middlebank, and May 1996 for combined stations (Table 5.1; Appendix 14). Due to the low numbers in samples, the exact size at the onset of flexion could not be determined. At 4.0 mm BL the notochord was still straight, by 5.0 mm BL it was clearly bent, and the process was not yet complete at 6.2 mm BL in the largest specimen caught. Clearly most larvae were in the preflexion stages, but despite poor representation several size classes and developmental stages were frequently found together (Appendix 15).

Temporal Statistics

For the most part, probably as a result of low concentrations, there was no statistical evidence of seasonality. Of the 30 species tested, only seven species registered significant differences in concentrations between the seasons over Middlebank (Table 5.3). These were *S. sagax*, *G. capensis*, *P. olivaceum*, *A. argyrozona*, *D. s. capensis*, *T. t. capensis* and Gobiidae Species 1. Of

Table 5.3 - Results of the Kruskal-Wallis single factor ANOVA by ranks for seasonal distribution of fish eggs and larvae and squid para-larvae at Middlebank and for all stations combined sampled between August 1993 and October 1996 (* denotes a significant difference at the 95% level; 1, 2, 3 & 4 represent summer, autumn, winter and spring respectively).

	Middlebank				Combined Stations			
Source	H-value	Sig. level	Ranking	Absent	H-value	Sig. level	Ranking	Absent
Total larvae	7.14	0.078	3>4>1=2		10.57	.014*	3>4>2=1	
Engraulis japonicus	4.49	0.213	1>4>2=3		2.67	0.445	4>1>3=2	
Etrumeus whiteheadi	2.99	0.393	4=3>2=1		7.86	.049*	4>3>2>1	
Sardinops sagax	17.07	0.001*	3>4>2>1		13.74	.003*	3>4>1>2	
Lampanyctodes hectoris					8.27	.041*	3>2>4	1
Gaidropsarus capensis	10.51	0.015*	3>2=4	1	15.9	.001*	3>2>4	1
Merluccius capensis	1.61	0.657	2>4>3	1	1.74	0.627	3>4>2>1	
Gobiesocidae Sp1	2.63	0.452	4>3	1, 2	6.74	0.08	4>3	1, 2
Gobiesocidae Sp2	1.45	0.693	3>2	1, 4	2.81	0.422	4=3>2	1
Coccotropsis gymnoderma	1.69	0.637	4>2>3>1	1	3.65	0.302	4>2>3>1	
Chelidonichthys capensis	2.25	0.522	3>1>2>4	4	4.52	0.211	3>4>2>1	
Pomadasys olivaceum	8.79	0.032*	3	1, 2, 4	15.03	.001*	3>2	1, 4
Argyrozona argyrozona	8.24	0.041*	3>4=1=2		6.93	0.074	3>4>2>1	
Chrysoblephus laticeps	5.64	0.13	4>3	1, 2	4.67	0.197	4>3>2	1
Diplodus sargus capensis	9.89	0.019*	3>4	1, 2	17.64	.001*	3>4>2	1
Pagellus bellotti natalensis	6.73	0.081	3>1	2, 4	10.45	.015*	3>1>2	4
Spondyliosoma emarginatum	4.5	0.212	4	1, 2, 3	10.31	.016*	4	1, 2, 3
Sparidae Sp6	3.05	0.384	4=1	2, 3	4.48	0.214	4>1=2	3
Sparidae Sp11	4.24	0.237	3>4	1, 2	5.82	0.121	3>1=2=4	
Trachurus trachurus capensis	10.28	0.016*	3>4	1, 2	8.68	.034*	3>4>2	1
Cheilodactylidae Species 1	4.97	0.174	3>4>2	1	12.37	.006*	3>2>4	1
Parablennius pilicornis	5.99	0.112	4>3>1>2		11.07	.011*	4>3>1>2	
Blenniidae Sp4	5.95	0.114	4>3	1, 2	6.97	0.073	4=3>1	2
Blenniidae Sp5	1.16	0.763	1>3>4>2		3.24	0.356	1=4>3>2	
Paracallionymus costatus	1.26	0.739	1>4>2>3		1.27	0.736	4>3>2=1	
Gobiidae Sp1	11.59	0.008*	3>4>1	2	9.86	.019*	3>4>2>1	
Gobiidae Sp2	4.49	0.213	2	1, 3, 4	1.91	0.592	2>4>3	1
Gobiidae Sp3	1.45	0.693	3=2	1, 4	6.32	0.097	3>4=2	1
Cynoglossus zanzibarensis	1.32	0.724	2>4=1=3		3.45	0.328	4>3>2>1	
Austroglossus pectoralis	1.93	0.587	4>1>2>3		5.6	0.133	4>1=2>3	
Heteromycteris capensis	5.3	0.151	1>4>2	3	3.25	0.355	4>1>2>3	
Fish eggs	4.74	0.192	1>3=4>2		5.74	0.125	1>4>3>2	
Loligo vulgaris reynaudii	2.14	0.543	2	1, 3, 4	1.07	0.784	4=3=2	1

these. *P. olivaceum* was only present in winter. while *D. s. capensis* and *T. t. capensis* were caught only during winter and spring months. All seven of these species were present in significantly higher concentrations in winter. When concentrations for each species from all stations combined were analysed. 12 species exhibited a significant seasonal difference (Table 5.3). Of these. nine species (*S. sagax*, *L. hectoris*, *G. capensis*, *P. olivaceum*, *D. s. capensis*, *P. b. natalensis*, *T. t. capensis*. Cheilodactylidae Species 1 and Gobiidae Species 1) were most prevalent in winter. The remaining three (*E. whiteheadi*, *S. emarginatum* and *P. pilicornis*) were more abundant in spring. Amongst these. *P. olivaceum* was represented only in autumn and winter. and *S. emarginatum* was only present in spring. The overwhelming concentrations caught in August 1993 had a strong influence on the seasonal pattern of total larvae. On Middlebank. winter produced the most larvae followed by spring. summer and lastly autumn. The differences were. however. not significant (Table 5.3). Looking at all stations combined. winter still was dominant followed by spring. autumn and summer. In this case. however. both winter and spring catches were significantly higher than those in summer and autumn (Table 5.3).

There was no significant difference in the concentrations of eggs for either Middlebank or overall (Table 5.3). although summer was represented the best and autumn the least in both cases. Winter and spring concentrations were similar over Middlebank. but for combined stations. spring saw greater catches than winter. This shows that there is a consistent production of eggs throughout the year in all types of conditions. If the eggs could have been identified to species level. seasonal differences for some. as in the case of the larvae. may well have been significant. Squid para-larvae did not register any seasonal trends (Table 5.3). although poor catches were most likely the cause of this.

DISCUSSION

While routine biological sampling may provide information on the timing of spawning in fish based upon GSI's (De Vlaming . Grossman & Chapman 1982) as well as macroscopic structure of the gonads. they give no real indication of spawning (Hare & Cowen 1993). The presence of ripe gonads in adult fish indicates the intent to spawn. However. if the environmental (and often oceanographic) conditions are not met then spawning may be delayed or aborted altogether. The only real proof of a spawning event is given by observing post ovulatory follicles in histological preparations of gonads or by the presence of eggs and larvae. There is evidence that certain fish spawn at a specific time and place to take advantage of conditions which ensure the retention of

eggs and larvae in a predetermined geographic location, e.g. Lobel (1978), Ralston (1981) and Randall (1961). In *Chaetodon miliaris*, females produce one batch of eggs which are released all at once when it perceives conditions for the survival of its propagules to be optimal (Ralston *op. cit.*). So while standard sampling techniques provide an indication of a spawning season, the exact time of spawning can only be determined from intensive histological preparations or egg and larval surveys.

Being situated in a temperate zone, the environment in the study area is extremely variable. Although conditions can be considered relatively stable from year to year, water temperatures, degree of mixing and winds are highly variable between seasons within each year. The timing of reproduction is therefore crucial to species survival, and an understanding of this process would also lead to a greater appreciation of the ecology of those species concerned (de Vlaming 1972). For example, from the presence of newly spawned eggs in the plankton it was determined that the pilchard, *Sardina pilchardus* spawned at night in an effort to reduce predation on the eggs by diurnal planktivores (Ré, Farinha & Meneses 1989). Also, the formation of local populations of herring in the Baltic was attributed to the spawning of adults during precise population-specific temperatures and periods in spring and autumn when temporal larval survival zones with favourable nutrient levels were present (Ojaveer & Raid 1989). In the North and Irish Seas the distribution and presence of cod eggs and larvae in samples (Brander 1989) showed that the timing and location of spawning was probably linked to the processes of primary and secondary production on a small spatial scale of only a few nm. The majority of samples for this study were obtained while working from *Natpark Aonyx* where equipment for measuring physical parameters was not available. Most samples were only accompanied by sea surface temperature readings. However, detailed readings of physical parameters were obtained during the R.S. *Africana* voyages and their relation to larval concentrations and distribution will be discussed at a later stage (Chapter 6).

The locality and mode of spawning have been identified as factors which greatly influence the distribution and composition of larval fish assemblages (Leis 1993; Loeb, Kellerman, Koubbi, North & White 1993). The majority of fish species in Antarctic waters are demersal or benthopelagic and this is reflected in the distribution of eggs of those species which have been studied (Loeb *et al. op. cit.*). Free demersal and benthopelagic eggs are thought to have

evolved as a mechanism to avoid near surface waters which contain drifting and freezing ice (Kellerman 1989 in Loeb *et al. op. cit.*), a step which has been taken further by certain species, such as *Trematomus bernacchii* which lay eggs in guarded nests (Moreno 1980). Diving observations between 30 and 40 metres in South Bay on the Palmer Archipelago revealed that female *T. bernacchii* guarded eggs which they had laid in the cavities of the rosellid sponge *Rosella nuda*.

Although Leis's discussion on this issue (Leis 1993) revolves around coral reef species, much of the argument can be equally applied to the neritic fauna encountered during this study. Species which spawn benthic eggs on inshore subtidal reefs already decrease the chances of widespread dispersal, whereas those with pelagic eggs would be prone to advection or dispersal away from the source. While this may be part of the overall life history of some species, i.e. widespread dispersal and an ability to survive a wide range of conditions or initial dispersal from the reef environment followed by an active return mechanism prior to metamorphosis, those with more specific requirements during the pelagic phase as well as later during the settlement phase may find themselves at a disadvantage if they are moved too far and into an environment not suited to survival. The collection of various reproductive strategies employed by coral reef species ensures that few plankton surveys reflect the same taxonomic composition of adult fish on nearby reefs (Leis *op. cit.*). A similar scenario is not impossible where the nearshore is characterised by major high profile reef areas interspersed with sand, and the offshore region beyond is dominated by low profile reef and soft sediments. Species whose adults are not reef associated but exist as pelagics do not have too many restrictions on where to spawn. The source of eggs and larvae is less restricted but more difficult to determine, and their larvae are often more widespread, being largely dependent on the distribution of the adults (Young, Leis & Hausfeld 1986; Leis *op. cit.*).

The South-East Coast Ichthyoplankton Species Assemblage

In the following section, species are discussed in the same order they appear in Table 5.1, which conforms to the taxonomic arrangement used by Smith & Heemstra (1986).

Etrumeus whiteheadi, which is endemic between Walvis Bay and Durban, spawns all year round off South Africa with peaks from August to October (Shelton 1986). Larvae were absent in the months of May, July and December during this study but were present in all other months.

While no clear pattern of seasonal dominance was evident over Middlebank, samples from a wider range of sites revealed a winter/spring dominance which conforms nicely to the previously reported spawning habits (Shelton *op. cit.*). Brownell (1979) reported sampling eggs of *E. teres* all year round on both sides of the Cape Peninsula, but there is a chance that these were in fact *E. whiteheadi* as the distributional range of *E. teres* in southern African waters has been reported only as far south as Durban. If this is the case then it would appear that the species is capable of spawning all year round along most of the coast. If it was indeed *E. teres* then it serves to illustrate how closely related species exhibit similar patterns of reproductive activity and leads one to assume that requirements for larval survival are similar.

As one of the mainstays of the pelagic purse-seine fishery (Armstrong & Thomas 1989; Payne & Crawford 1989), most aspects relating to the life history and exploitation of *S. sagax* have been dealt with. From the Benguela system and Namibian waters it has been reported that they spawn all year round, peaking in spring and summer, with larger individuals spawning more often and for longer periods than smaller ones (Le Clus 1987, 1989). Batch spawning over a protracted period like this increases the chances of larval survival when favourable conditions predominate. Further south Shelton (1986) reported peak spawning between October and January and again during July and August. A similar scenario was observed for this species off the coast of southern California between 1978 and 1986, with year round spawning and peaks in summer and autumn (Watson 1992). In earlier years (1950s) the spawning season off California peaked sooner in spring and summer (see Ahlstrom 1967) perhaps due to cooler waters predominating or the influence of a different, more northerly stock (Lavenberg, McGowen, Jahn, Petersen & Sciarrotta 1986). Limited data from research voyages during the months of November along the south-east coast of South Africa revealed high densities of eggs, but information for the remainder of the year was lacking and the peak spawning season could not be determined. Evidence of reproductively active animals along the east coast off KwaZulu-Natal (KZN), however, points to a winter spawning peak (van der Elst 1990). With the exception of October, larvae were caught from all months at some stage during this sampling program, but the presence of the greatest concentrations during winter months agrees with the suspected winter peak along the east coast. This contrasts directly with the spring and summer peaks experienced in the northern Benguela system and is only in partial agreement with the bi-modal peak observed in the southern Benguela. The analysis of plankton data between 1953 and 1975 (Judy & Lewis 1983) illustrated that the seasonal distribution and abundance of eggs and larvae of the clupeid *Brevoortia tyrannus* coincided with the seasonal

distribution of the adults. Spawning also appeared to be all year round with September being the only month in which larvae were not represented in catches, a scenario similar to that of *S. sagax* in this study. The cooler waters off the west coasts of California and southern Africa could be the determining factor behind a west coast summer peak, with warmer waters on the east coast facilitating the peak shift to winter.

Engraulis japonicus spawns mainly between October and February in waters above the thermocline between Cape Columbine in the west and East London in the east, with the peak activity taking place from Cape Point to Cape Agulhas over the western edge of the Agulhas Bank (Crawford 1980; Shelton 1986; Shelton & Hutchings 1990; Shelton *et al.* 1993). Le Clus & Kruger (1982) reported a similar start to the spawning season in northern Namibian waters, but their data also revealed a more protracted season into autumn. Juveniles begin to recruit to the west coast fishery from around February (Prosch 1986). The large concentrations of eggs caught during this study in October 1995 conforms to this pattern. The absence of eggs from almost all samples may be explained by many spawning events, each lasting only a few days followed by rapid incubation and subsequent post-hatch growth. However, the presence of a large size range of larvae in most cases suggests a more prolonged spawning period, with retention taking place. It is therefore probable that the eggs are normally spawned further afield and the larvae then actively congregate within the sample area. The presence of the high concentration of eggs in October 1995 may have been the result of an unusually large spawning event taking advantage of conditions which were prevailing outside of their normal spawning area. The absence of anchovy eggs in catches from January 1991 to July 1992 led Tilney & Buxton (1994) to state that *E. japonicus* most likely does not spawn inshore along the south-east coast. We now know that they do indeed spawn inshore and that a prolonged sampling regime is required to take note of chance events such as this. While the highest concentrations of larvae between November and January indicate a peak summer season, anchovy larvae were caught from all months of the year with the exception of September which was only sampled once in 1994. No significant difference between seasonal concentrations means that while production may be concentrated around the summer months, anchovy are capable of spawning all year round, taking advantage of conditions suitable for larval survival at any time.

Most clupeiforms are pelagic, inshore fishes (Whitehead & Wongratana 1986). All clupeiform species found in this study have previously been investigated with respect to the

offshore distribution of larvae between the Tugela River and Algoa Bay on the eastern seaboard of South Africa. Larvae from all three species were found to be most abundant over the continental shelf in 50 to 100 metres of water (Beckley & Hewitson 1994).

While larvae of *S. sagax* in the study area conformed to this pattern, those of *E. whiteheadi* were sparse or absent at the offshore sites. The preference of *E. whiteheadi* larvae for the shelf waters (Beckley & Hewitson *op. cit.*) extended only as far south as East London. Further west at Algoa Bay, highest concentrations were at 500 metres on the shelf-break. It is feasible therefore that this offshore trend continues to Storms River, where the shelf-break is approximately 90 km offshore, well outside the limits of the sampling area in this study. Although larvae of *E. whiteheadi* are found close inshore off southern Namibia, highest concentrations are also offshore beyond the slope of the continental shelf in 500 metres (Olivar & Fortuño 1991). Findings by Beckley (1994) proved inconclusive as concentrations of larvae from Algoa Bay and Plettenberg Bay were too low to confirm any patterns observed here. In addition, the distance sampled offshore (60 km) was far greater than the maximum of 15 nm in this study. In the study by Watson (1992) of *S. sagax* distribution in southern California, the majority of larvae were found between the 22 and 45 metre isobaths with the lowest concentrations coming from the sites closer to shore in shallow (6 - 9 m) waters. Primary production measured as phytoplankton biomass, and zooplankton levels tend to be greater closer inshore off the California coast (Lasker 1978; Barnett & Jahn 1987), providing an ideal survival zone for eggs and first feeding *S. sagax* larvae. Samples were, however, only taken at a maximum distance of 7 km offshore in 75 metres of water, making any direct comparisons with this study's patterns difficult.

The eggs and larvae of engraulids are known to lack any significant degree of motility (Power 1986) which makes them extremely susceptible to drift away from a spawning site. *Engraulis mordax* spawns in the nearshore region in the Southern California Bight where food concentrations are optimal for first feeding larvae (Lasker 1978). However, the susceptibility of larvae to being passively displaced by offshore directed Eckman transport can lead them away from this survival zone and into one where the two major causes of larval mortality, predation and starvation (Hunter 1981), can result in recruitment failure and extreme population fluctuations. The occurrence of *E. japonicus* mainly inshore in this study, over central shelf waters off Algoa Bay and Plettenberg Bay (Beckley 1994), and close inshore along the West Coast (Shelton 1986) may indicate a similar life style to its northern

hemisphere counterpart with offshore Eckman transport leading to mass mortalities. Tilney *et al.* (1996) reported significantly higher concentrations of anchovy larvae at their offshore (3.83 km) station when compared to inshore (0.35 km), with more being found over sand substrates when compared to reef, although this difference was not significant. A direct comparison is difficult as the inshore station (Middlebank) in this study is not much closer to the shore than their offshore sites. The absence of *E. japonicus* larvae from samples taken in the Agulhas Current during R.S. *Africana* voyage #099 (Beckley *op. cit.*) may also indicate an avoidance of oceanographic features which can rapidly displace them from their points of origin into unknown areas which may not be suitable for survival.

The frequent appearance of flexion and postflexion *E. japonicus* larvae in catches could be an indication that like other anchovy species such as *Engraulis mordax* (Power 1986; Theilacker & Dorsey 1980 in Morse 1989), *E. japonicus* is a slow swimmer making it susceptible to capture irrespective of size. None the less, the fewer numbers of these larger larvae may indicate a movement away from the other congregated size classes in the sample area.

Based on the smallest individual sampled off Namibia by Olivar & Fortuño (1991), size at hatching for *E. whiteheadi* is around 3.7 mm BL, but recently hatched yolk-sac larvae from this study measuring 3.0 mm BL show that the different conditions between east and west coast undoubtedly affect developmental times and sizes. This hatching size is larger than for *E. japonicus* and would explain the pattern of larger mean sizes seen for this species. While other herring species such as *Clupea harengus* (Theilacker & Dorsey 1980 in Morse 1989) are regarded as fast swimmers, this is perhaps not the case for *E. whiteheadi*, except in large postflexion animals, as the majority of larvae caught were in the flexion stage of development and capable of active swimming. The absence of postflexion *E. whiteheadi* larvae could indicate that they were actively evading capture or had moved to deeper offshore waters prior to metamorphosis. The paucity of yolk-sac stages is likely indicative of loss due to extrusion, while the wide size ranges of larvae in samples indicates retention in the immediate spawning area. In the case of *S. sagax*, the paucity of larger postflexion larvae may have been due to movement away from the sample area rather than avoidance as sardine larvae, e.g. *Sardina pilchardus*, are generally classed as weak swimmers (Theilacker & Dorsey 1980 in Morse 1989).

The only information that could be found on the reproductive habits of *Gonorhynchus gonorhynchus*, states that it breeds in deep water and the pelagic young are often preyed upon by seabirds (Smith 1986a). In the review by Richards (1984) no mention was made of the eggs of this genus, while the larvae of *G. abreviatus* (Okiyama 1988, page 140) and *G. greyi* (Bruce 1989a) have been described. Olivar & John (1987) described five larvae of *G. gonorhynchus*, all of which were either postflexion or transforming larvae ranging in size from 21.9 to 51 mm BL. All were sampled from the south-east Atlantic, with four caught in surface tows in March 1971 and one from an oblique tow in June 1983. There was no indication of growth rates for larvae of this species or *G. abreviatus* in the literature. The single specimen identified in this study was initially assumed to be late postflexion, measuring 71.13 mm BL, captured in November 1994. However, if the 51 mm SL larva described by Olivar & John (*op. cit.*) was already transforming then this one must be considered a juvenile. A conservative estimation of 72 hours' egg incubation time and three months growth would mean the individual was spawned somewhere around the beginning of August 1994.

The larvae of *Diogenichthyes atlanticus*, whose adults are mesopelagic, were found to be present over most of the continental slope area and at most times of the year in the Benguela system (Olivar 1988a). In this study, one larva was caught inshore at Rheeders in August 1993 and measured 4.5 mm BL, indicating that it was most likely spawned during July. The second individual was caught offshore from Elands River in October 1995 and measured 4.4 mm BL meaning it was most likely spawned in early September. The mesopelagic habitat occupied by the adult fish is likely to be in areas far offshore where the depth exceeds 150 metres. This would mean spawning grounds are a great distance from these sample sites. The two larvae captured were probably strays separated from the rest of the cohort and transported into the area by onshore winds or currents.

Lampanyctodes hectoris is the most common of the lanternfish in our waters and is commercially important in the south-east Atlantic for fishmeal production (Hulley 1986). Size at notochord flexion for *L. hectoris* ranges between 6.4 and 7.7 mm BL in the Benguela system (Olivar & Fortuño 1991). All specimens > 5.7 mm BL caught in this study showed signs of flexion, indicating regional differences in developmental rates. Based on egg and larval surveys in the southern Benguela (Prosch 1991) adults reach a spawning peak in late winter and spring (August-October). A similar pattern was originally found by Olivar (1985 in Olivar & Fortuño *op. cit.*) for

this species between the Cape of Good Hope and the Cunene River in the north, with maximum concentrations being caught beyond the 200 metre isobath. All larvae from this survey were caught offshore at five or ten nm from Storms River in waters between 90 and 105 metres, with none being sampled over Middlebank at 1.4 nm offshore and a maximum depth of 60 metres. The majority of larvae were caught between April 1995 and October 1995 with a peak in July 1995, making winter catches significantly higher than those from other seasons (none were caught in summer months). This pattern is similar to that from the west coast, and although they appear to be caught in shallower waters (< 105 m), their preferred distribution cannot be determined as deep-sea stations were not sampled in this study. The adults of *L. hectoris* are described as pseudo-oceanic species (Hulley 1986) and as such it was no surprise that none of their larvae were caught inshore during this study. In a survey by Beckley (1994) all myctophids caught along transects off Algoa Bay and Plettenberg Bay were grouped together and found to be most prolific at offshore stations. The distances offshore were, however, far greater than in this study as they sampled sites to beyond the shelf-edge up to 150 km from shore at Plettenberg Bay. A similar pattern was observed along the west coast where *L. hectoris* larvae were encountered from the 150 m isobath out to depths of over 1 000 m (Olivar & Fortuño *op. cit.*; Prosch 1991).

Four specimens of *Symbolophorus barnardi* were caught in October 1995 off Elands River in 110 metres of water. All were preflexion individuals measuring between 4.3 and 4.8 mm BL. Flexion in this species is reported to be around 7.0 mm BL (Olivar & Beckley 1994a). The size of these larvae together with the sample time indicate a spawning time around the beginning of September which conforms to previous reports of their abundance in spring months in the Agulhas Current (Olivar & Beckley *op. cit.*).

According to Hulley (1986) three *Hygophum* species occur in the study area, namely *H. hanseni*, *H. hygomii* and *H. proximum*. The larvae of these three together with those of *H. bruuni* and *H. macrochir* have been sampled in the Benguela system (see Olivar & Fortuño 1991) during both summer and winter months (Olivar 1988a). The two larvae sampled during this study were from a ten and a five nm station and were preflexion larvae measuring 5.5 mm BL and 4.6 mm BL. Spawning would have taken place in the winter months of June/July, perhaps in an attempt to avoid the upwelling season - a characteristic which is evident in many myctophid species (see Olivar & Fortuño *op. cit.*).

Eggs of *Gaidropsarus capensis*, which is endemic between Cape Town and East London, appear all year round in waters on both sides of the Cape Peninsula (Gilchrist & Hunter 1919; Brownell 1979). The pelagic existence of these fish lasts about two months after which they assume a benthic lifestyle under stones (Brownell *op. cit.*). No larvae were found in summer months during this study, but they were frequently found, albeit in low concentrations, during all other months of the year. This total absence in summer could indicate a variation in spawning habits between individuals from the south and east coasts, although the absence of *G. capensis* larvae in summer is not unusual for this group of fishes. Other gadids such *Urophycis regia* spawn between October and May in the Middle Atlantic Bight (MAB) with no trace of eggs or larvae in summer, while others such as *U. floridana* and *U. cirrata* were found in winter only in the same region (Comyns & Grant 1993). Of all the gadid species studied in the MAB, only *U. chuss* showed evidence of summer spawning. Cohen (1986a) states that adult *G. capensis* are confined to a habitat extending from tide pools down to 50 metres. While this may reflect a function of the depth limit for effective collection by SCUBA, one can also assume that deeper distribution records would have been noted from research trawls which are capable of capturing small sized fish once the net becomes clogged. The upwelling in summer and the net movement of water offshore may preclude closure of the life cycle of *G. capensis* if a cryptic habitat cannot be found. By not spawning during this period, this potential source of massive mortalities could be avoided. The pattern of offshore distribution observed for *G. capensis* in this study was not expected in terms of the retention theory. Due to their inshore habitat (Cohen *op. cit.*) their larvae would not be expected as far out as five or ten nm in water between 98 and 102 metres deep. Comparing the wide spread distribution from Middlebank to ten nm offshore with findings from other studies is difficult as no specific distances offshore are mentioned. Both Gilchrist & Hunter (1919) and Brownell (1979) reported eggs from around the Cape Peninsula, but give no indication of how close inshore or far offshore the samples were taken. Only two larval specimens were reported from Benguela surveys (Olivar & Fortuño 1991) and both were caught between the 150 and 200 metre isobath. Looking at the distribution map and the site co-ordinates for these larvae a rough estimate of distance offshore would be anywhere from five to fifteen nm.

It would appear as if other representatives of the family Gadidae, even those within the same genus, display a wide range of distributional patterns. Working on larvae of the *Urophycis* and *Phycis* genera caught along offshore transects off New Jersey and Virginia in

the MAB, Comyns & Grant (1993) found a high degree of interspecific variation. Larvae of *U. chuss* were found along the entire transect with lowest concentrations inshore (< 40 m) and highest levels between 40 and 120 metres over the mid-shelf region. A seasonal trend was observed for *U. regia* whose larvae were concentrated over the mid-shelf (41 - 43 m) in autumn and offshore (> 100 m) in winter. Larvae of *U. tenuis* were collected at all stations except those closest to the shore. Spawning appeared to have taken place out over the shelf-break with a gradual size increase in larvae as sites approached the shore, indicating a shoreward migration to nursery areas. Both *U. floridana* and *U. cirrata* were only found offshore in winter, but their size indicated that they were probably spawned offshore in the South Atlantic Bight and transported north. The last species they describe, *P. chesteri*, was only caught in surface waters offshore, with sizes indicating they were spawned in the near vicinity as well. Distances are not quoted, but using grid references it would seem that the inshore stations were between 10 and 60 nm from shore, and offshore sites beyond the 100 m isobath which appears approximately 80 nm from the coast at its closest point. This also marks the starting point of the shelf-break as the contours show a rapid decrease to 1 000 metres over a few nautical miles and then to 2 000 metres over the next 10 to 20 nm.

The size at hatching for *Merluccius capensis* recorded by Matthews & De Jager (1951) was 2.35 mm BL, and the smallest specimens sampled in the Benguela system (Olivar & Fortuño 1991) were 2.6 mm BL. The small yolk-sac larvae sampled during this study (1.6 - 1.9 mm BL) therefore appear to represent a regional variation in size at hatching. Sampling soon after a spawning event such as in August 1993, produced 26 *M. capensis* larvae, all of which were small preflexion animals. The absence of larger animals therefore does not necessarily mean they could not be caught, but that the cohort had not yet attained the later developmental stages. Illustrations from Haigh (1972a) show that flexion has begun in larvae of 6.8 mm SL, with Olivar & Fortuño (*op. cit.*) placing it around 7.0 - 8.0 mm SL. The spawning season for *M. capensis* has been quoted as being between September and January in midwater over a large area offshore (Cohen 1986b), while van der Elst (1990) states that spawning fish are found all year round with activity peaking in August and September. Spawning appears to be confined to a shorter season for other species, e.g. *Merluccius productus* migrates southwards towards California in autumn (Hollowed 1992) to spawn off Los Angeles and the Baja Peninsula, reaching a peak between January and March. While larval abundance during this study was found to be fairly evenly distributed throughout the seasons,

the winter and spring months did deliver slightly higher concentrations. Adults are distributed around the coast of southern Africa to a depth of approximately 400 metres (Cohen *op. cit.*) and as such they are subject to a wide range of environmental and physical conditions. It is suggested that species such as these would be able to adapt the timing of reproduction to match favourable conditions whenever they arise, hence the presence of larvae throughout the year.

Physiculus capensis is endemic to the shores of southern Africa extending from southern Namibia to East London (Cohen 1986c; Macpherson 1986 in Olivar & Fortuño 1991). Collections by Brownell (1979) on the Atlantic side of the Cape Peninsula contained eggs of this species in April and July and from September to November. Sampling in the southern Benguela system between 1983 and 1985 revealed larvae in January when upwelling was strong and June/July when this process was quiescent (Olivar & Fortuño *op. cit.*). Three *P. capensis* larvae were captured in night samples off Elands River in October 1995. According to previous descriptions in the literature (Brownell 1979), the largest of these (4.7 mm BL) may well be the biggest larval specimen yet sampled anywhere. There were no signs of flexion. These individuals would have been spawned around the beginning of September, before the start of the south-east coast upwelling season. The low numbers of this species may be attributed to the distribution of adults over the continental shelf and upper slope, far from the study area.

The entire life cycle of *Bregmaceros atlanticus* achieves closure in the open water environment where the adults, like the eggs and larvae, are oceanic and pelagic (Houde 1984; Smith 1986b). This may explain the paucity of larvae in the study area which was situated within the neritic region. Information on the timing of spawning is lacking, but larvae have been described from other parts of the ocean. They hatch at around 1.5 mm NL, and from illustrations in Houde (*op. cit.*) and Okiyama (1988) flexion appears to start anywhere between 7.0 and 10.0 mm NL. All five specimens caught during this survey were either late postflexion or early juveniles. Of interest were the three caught over Middlebank (28/03/94) measuring 15.49, 18.86 and 27.77 mm BL. This size range illustrates the similar habitat occupied by larval and juvenile stages, as they came from the same sample area at the same time. Growth rates of early stages are not known, but indications from the sizes and sample times are that spawning probably occurs around January/February and again in June/July.

Indications from some of the first ichthyoplankton surveys in the Cape (Gilchrist & Hunter (1919) and from later studies based on gonad state of adult fish (Hecht 1976; Payne 1977; Japp 1989) were that the peak spawning season for the endemic (between Walvis Bay and Algoa Bay) *Genypterus capensis* was late winter and spring. Based on the presence of eggs in waters on both sides of the Cape Peninsula, Brownell (1979) stated that *G. capensis* had an extended spawning season from March to November, with a possible peak in May and June. This was backed up by Olivar & Sabates (1989) who found larvae from April through to November/December with peak concentrations in mid-year on the south-western Agulhas bank, when sea surface temperatures were lowest. Along the west coast they again found this species to exhibit an extended spawning season with larvae appearing around May and being caught regularly until November, with a peak from July to September when upwelling was the least active. Only three larvae were caught during this survey, two of which were caught during the months of August and October, conforming to the winter/spring peak previously reported for the species in the area. The third specimen, a large postflexion or transforming larva measuring 24.0 mm BL, was caught in April. Conservative estimates would place the time of spawning around the beginning of February, further extending the already protracted spawning season previously thought to begin only in March.

The lophiiform fishes lay one to three eggs in hexagonal shaped liquid-filled chambers arranged in irregular layers within a protective sheath of gelatinous mucous, collectively known as an egg-raft (Pietsch 1984). Descriptions of early life history stages are, however, lacking with only three of approximately 25 lophiid species described worldwide. The illustrations of specimens identified as *Lophius* spp. from the Benguela system which appear in Olivar & Fortuño (1991) closely resemble the single preflexion 4.5 mm BL larva captured in October 1995 during this survey. Whether this was *L. vomerinus* or the Monk *L. upsicephalus* is unknown although distributional records for adults (Caruso 1986) would increase the chances of it being the latter.

The Gobiesocidae lay demersal eggs which are attached to the underside of rocks or shells or on kelp fronds (Allen 1984) and which are guarded by the males in most cases. Apart from a brief description of eggs and yolk-sac larvae of *C. dentex* by Gilchrist (1916) which did not include illustrations, and an illustrated description of what was assumed to be *Lecanogaster chrysea* sampled near the Cunene River mouth (Olivar 1987d), none of the southern African gobiesocids have been dealt with. Based on larval presence, Species 1, which was the most abundant, was a

winter/spring spawner. Winter and spring were still peak months for Species 2, with small numbers being caught in autumn. Only five larvae of the third species were caught, two in October 1995 and three in April 1996. It may be significant, even though numbers of Species 3 were low, that like *L. chrysea* from Namibian waters, none of the gobiesocid larvae were found during the summer months. The gobiesocids were one of the most dominant groups in samples from a previous offshore transect survey (Tilney *et al.* 1996), where they were found to be significantly more abundant inshore (0.35 km) as opposed to offshore (1.26 and 3.83 km), with a degree of retention over reef areas being apparent. No gobiesocid larvae were found at offshore sites during this study. The overall poor representation of gobiesocids in samples may be the result of demersal eggs preventing widespread dispersal such that emergent larvae are located in patchy congregations.

A maximum size at hatching in the gobiesocids has been recorded from wild caught eggs at Santa Catalina Island, California, at 6.1 mm BL (Allen 1979). None of the small (2.6 - 2.9 mm BL) specimens caught during this study were yolk-sac stages, and it is assumed that they emerge at a smaller size. Caudal flexion for most Indo-Pacific species is at around 3.8 - 4.4 mm BL (Leis & Rennis 1983) and between 5.0 and 6.0 mm BL for *L. chrysea* sampled off the Cunene River (Olivar & Fortuño 1991). These figures compare well with the 4.3 mm BL for Species 1 and 4.9 mm BL for Species 2 in this study. Recently hatched larvae may still be close to the substrate after hatching from benthic eggs (Leis & Rennis *op. cit.*) which would preclude their capture, while larger larvae approaching settlement and metamorphosis may well be close to the substrate once more in search of suitable habitat. The mean sizes of Species 2, which were generally the largest of the three species, could either indicate a larger size at hatching or a period associated with the substrate after emergence before they enter the pelagic realm.

The dories, which have had their larvae described and which are found in southern African waters include *Zenopsis conchifer* (Weiss, Hubold & Bainy 1987) and *Zeus faber* (Clark 1914; Sanzo 1931 in Olivar & Fortuño 1991; Crossland 1982). A few other species have been described from elsewhere in the world (see Tighe & Keen 1984) but information on the eggs and larvae of most species is lacking. The few larvae from this study resembled *Z. faber*, but since the closely related and co-occurring endemic *Z. capensis'* larvae have not been described, their identification was considered tentative. All larvae were captured within two nm of shore between June and August. Due to the benthic existence of adults further offshore, which supposedly spawn mainly

during the summer months over the continental shelf (see van der Elst 1990), these larvae were probably strays, spawned sometime during April or May.

Although *Syngnathus acus* is the most common pipefish in South African estuaries (Dawson 1986), it also occurs offshore to depths of at least 100 metres. Due to the lack of any commercial importance within this group of fishes, except perhaps in the aquarium and curio trade, literature dealing with their early life history is limited (Fritzsche 1984). Adult males have a special pouch which is used to receive and incubate eggs. In some species larvae are also retained until they have reached the metamorphosis phase and are then released as juveniles. The early development of *S. acus* is not known and the two specimens captured (30.2 mm and 58.3 mm BL) were most likely juveniles, not larvae. With no knowledge of incubation times or growth rates of larvae, determining the timing of spawning was not possible.

Coccotropsis gymnoderma is a small endemic waspfish found from the Cape to Algoa Bay, reaching a maximum size of around 40 mm TL (Poss 1986a). Eggs of this species were collected in summer by Brownell (1979) in False Bay, and a total of 45 were collected in Tsitsikamma between January 1991 and July 1992 by Tilney & Buxton (1994), but no mention was made of their seasonality. Samples from this project did not conform to any pattern of spawning seasonality although highest concentrations were in spring and autumn, with November featuring twice as the most productive month. Larvae of this species were present in very low concentrations, but occupied sites at all transect stations except ten nm. While this distribution is patchy at best, the larvae reflect the known depth distribution of adults from two metres (Pers. Obs.) down to 108 metres (Poss 1986a). Their absence from collections at ten nm is most likely just a feature of the low concentrations and limited sampling rather than selective behaviour.

The horsefishes are represented by two endemic species in South African waters, *viz. Congiopodus spinifer* and *C. torvus* (Poss 1986b), both of which have similar distributional ranges from Walvis Bay in Namibia to KZN. The eggs of both species have been described and appear to be very similar (Gilchrist 1903, 1904, 1916; Gilchrist & Hunter 1919; Brownell 1979), but only the larvae of *C. spinifer* have previously been described (Gilchrist & Hunter *op. cit.*; Brownell *op. cit.*). The eggs of *C. torvus* described by Gilchrist (1903) were unfertilised ovarian eggs extracted from an apparently ripe female caught in a trawl. Attempts to fertilise eggs from this species were not

possible as ripe males and females were never caught at the same time. No reference is made as to when the ripe female was procured, so not much can be said about its reproductive seasonality. Fertilised eggs were obtained for *C. spinifer* when ripe males and females were caught in the same trawl at Buffels Bay on 25 November 1903 (Gilchrist 1904). Subsequent to this, Gilchrist & Hunter (*op. cit.*) found *C. spinifer* eggs all year round in Table Bay and assumed an all year round spawning pattern, later confirmed by Brownell (*op. cit.*) when he observed their eggs all year round at the Cape Peninsula. Four *C. spinifer* larvae, one flexion (8.4 mm BL) and three yolk-sac (2.5, 3.7 and 3.8 mm BL) were caught during this survey in September 1994. The low numbers and absence of larvae for the rest of the months could not be explained as high densities of adult fish have been observed during diving operations in the area.

The first descriptions of the endemic *Chelidonichthys capensis* larvae, although initially misidentified as *Trigla kumu*, were by Gilchrist (1903, 1916) and Gilchrist & Hunter (1919). Larvae were reared from eggs fertilised from ripe adults captured in December. Reports on the timing of spawning for this species vary, but overall they appear to be capable of spawning at any time of the year. While December to March, when water temperatures are warmest, was seen as the height of the spawning season for *C. capensis* in Namibian waters (Trunov & Malevanyy 1974), evidence of animals in spawning condition was found all year round. Larvae in later Namibian surveys were scarce (see Olivar & Fortuño 1991), with a few being caught in winter samples. In Eastern Cape waters this species was found to spawn between November and January and again during March/April (Hecht 1977), while van der Elst (1990) reported spring and early summer as the prime spawning times. The most recent study on *C. capensis* from the Agulhas Bank (M^{c}Phail 1997) showed peaks in the numbers of ripe and spent gonads in August, September and January, although spawning was evident in animals almost all year round. The only months in which larvae were not caught during this study were June, September and December. However, each of these months was only ever sampled once and it is possible that larval patchiness at those times precluded their capture. In all likelihood *C. capensis* spawns all year round in the south-east Cape, but indications from larval concentrations point to definite peaks in winter and spring months. This pattern reflects a species which is capable of reproducing anywhere at anytime should favourable conditions present themselves. The absence of *C. capensis* larvae at the 15 nm station could be construed as unusual since adults are found in waters anywhere from 10 to 390 metres deep (Heemstra 1986a), but patchiness of larvae may also have contributed to this.

Off the west coast of southern Africa, while larvae were not numerous in catches, they better reflected the known adult distributional range, being collected on both the shore- and oceanic-side of the 200 m isobath (Brownell 1979; Olivar & Fortuño 1991).

Haemulids are reported to hatch at a small size (Podosinnikov 1977), and amongst the small 2.5 mm BL larvae sampled in this study, none were yolk-sac stage, indicating a probable size-at-hatching for *P. olivaceum* of < 2.0 mm BL. Notochord flexion for Indo-Pacific haemulids, including several *Pomadasys* species, occurs between 3.9 and 5.4 mm BL (Leis & Rennis 1983), and *P. olivaceum* conformed to this pattern. The absence of any postflexion larvae in these samples could be ascribed to their ability to evade capture or because of early settlement, e.g. *Pseudopristipoma nigra* has fully developed fins at 5.7 mm BL and is thought to enter the settlement phase soon after (Leis & Rennis *op. cit.*).

Twenty-two species of adult and juvenile sparids were recorded in the study area by Buxton & Smale (1984). This number was increased by one with the addition of the santer, *Cheimerius nufar*, by Burger (1990). Larvae from 17 sparid species were tentatively identified by Tilney & Buxton (1994), while this study reports 14 species. While larvae of some of these were present infrequently and in low concentrations, others were well represented. The inability to capture specimens from all 23 species previously recorded as adults could reflect the unsampled intertidal and surf zone where certain sparid larvae may be retained for the duration of their larval life.

The spawning season of the endemic *A. argyrozona* is mainly in the spring and summer months (Nepgen 1977; Smith & Smith 1986; van der Elst 1990) but sometimes extends into March. Although reproductively active fish have been caught in the study area during these months, the peak is thought to be in February (Davis & Buxton 1996). The eggs and yolk-sac stages were initially described by Gilchrist (1903, 1916) for a species then referred to as *Dentex argyrozona*, after artificial fertilisation of eggs in December 1902. The presence of larvae in the study area eludes to a prolonged spawning season. While there was no clear seasonal distinction, concentrations from winter and spring months reflected peak activity. Detection of a summer maximum was not forthcoming and could have been either as a result of undersampling during these months or larval patchiness. Specific spawning behaviour for *A. argyrozona* is not known, but they are commonly caught in large numbers in waters up to 200 metres deep (Smith &

Smith 1986) and their larvae have been recorded from all four seasons. The reason for the absence of larvae from the 15 nm station, where the maximum depth was 113 metres, is not clear, although their appearance on only one occasion at 10 nm may point to an inshore spawning habit or inshore retention of early life history stages.

Captive rearing of *A. argyrozona* (Davis & Buxton 1996) revealed that hatched larvae measured 2.4 mm BL. Even with shrinkage, the 1.8 mm BL yolk-sac larva captured in the study area indicate that size at emergence under natural conditions is smaller. While fin elements were fully formed by 7.0 mm BL in captive reared specimens, complete ossification was only completed at 33.0 mm BL (Davis & Buxton *op. cit.*) corresponding to 71 days post-hatch. Based on these developmental rates, the range of sizes (1.8 - 4.5 mm BL) caught at one site in August 1993 during this study would have been representative of newly hatched individuals through to larvae approximately 19 days old. This provides strong evidence for active retention for at least this period within their area of origin.

Smith & Smith (1986) reflect that *Boopsoidea inornata*, which is endemic between the Cape and KZN, probably spawns in spring and summer, a sentiment echoed by van der Elst (1990) who adds that they appear to exhibit a similar reproductive biology to *S. emarginatum*, i.e. spawning between September and January (Penrith 1972). Whether this includes the complex nest building and egg guarding displayed by the *S. emarginatum* is not clear, but it is unlikely. All larvae were caught in October 1995 and ranged in size from 5.5 mm BL to a 8.5 mm BL flexion larvae with fully developed fin elements. Description of a spawning season based on these data is not possible, but their presence at least seems to agree with previously ascribed spawning times for the species.

Based on extensive surveys performed on adult fish from Cape Recife and the TNP, the spawning season for the endemic *C. laticeps* was determined to be from October to January (Buxton 1990). During this study larvae were detected as early as August in 1993 and as late as March in 1996, but there was no evidence that spawning was continuous for this duration. Indeed, no larvae were detected for the months November, December and January, although these months were not sampled intensively. According to Smith & Smith (1986) adult *C. laticeps* are found on reefs in waters up to 100 metres deep, so the occurrence of larvae at the five and ten nm stations in this study is not unusual although deep reef was never encountered at these distant stations. In addition, the fact that *C. laticeps* spawns at the surface (Buxton *op. cit.*; Buxton &

Garratt 1990) means that eggs are subject to extensive dispersal by wind driven surface currents, so the presence of larvae may not be a good indication of the origin of the material.

Larvae of *C. laticeps* reared in the laboratory, hatched at 1.76 mm BL (Davis 1996) with yolk absorption being completed just after the onset of first feeding at approximately 2.6 mm BL. This was the same size as the smallest wild caught specimen which had completed yolk-absorption. According to the illustrations from Davis (*op. cit.*) the flexion process starts in 4.95 mm BL larvae, slightly smaller than the 5.6 mm BL observed during this study. Bearing in mind the low concentrations overall, the small size range of larvae in any one sample may be indicative of a lack of retention as each batch of spawned eggs moves away from the original site of release. The variability observed amongst mean sizes with low deviations supports this, with mean sizes being larger during the second half of the study as more stations were sampled offshore and Middlebank was sampled less intensively. This provides further evidence of movement away from the reef area as larvae develop.

A single flexion larva of *Diplodus cervinus hottentotus*, which is endemic from the Cape to Sodwana Bay, was caught in November 1995. Using the sizes after hatching in Brownell (1979) this larva was estimated to be between three and four weeks old. This spawning activity in October complies with a previous study where eggs in False Bay were collected between October and January (Brownell *op. cit.*). Back calculation using Brownell's laboratory growth rates placed the spawning time of 10 to 20 mm SL juveniles found near Port Alfred (Christensen 1978) at around mid-August. This season of reproductive activity in the Eastern Cape was confirmed in a study on this species in the TNP (Mann & Buxton 1998) which showed that spawning took place between August and December, with a peak in October, precisely the time that the larva caught in this survey was thought to have been spawned.

The closely related *D. s. capensis* was more numerous. None were present in summer months but the species was generally well represented for the remainder of the year, particularly in winter. Adults sampled in the TNP (Mann & Buxton 1998) from the intertidal and shallow subtidal zone displayed peak gonad activity between August and October, with some evidence that a portion of the population was still active through summer until March. This discrepancy could be due to insufficient sampling during summer, or else a reflection of different spawning habits in different habitats, with the deep subtidal fish preferring the winter season in the absence of upwelling and when the water column is not highly stratified. Specimens sampled near St. Croix Island in Algoa

Bay (Coetzee 1986) and on reefs off KZN (Joubert 1981) exhibited reproductive activity from May to December. Based on egg distributions around the Cape Peninsula, Brownell (1979) detected a spawning peak over November/December with reduced activity for the remainder of the year. This year round activity is recognised by van der Elst (1990), but he quotes a longer peak period from mid-winter to early spring. Spawning of the closely related *D. sargus* from the Mediterranean takes place in spring between April and June (Ranzi 1933 in Brownell *op. cit.*). *Diplodus s. capensis* is found in estuaries, the intertidal zone, and subtidally where it prefers rocky ground down to depths probably not exceeding 25 metres (Smith & Smith 1986; Burger 1990; Mann 1992), a fact most likely related to feeding requirements. The absence from the 15 nm station could well be a reflection of their spawning pattern which appears to exclude the summer months (see above), but is more likely due to the restriction of adults and hence spawning in the inshore region. The larvae found at the five and ten nm stations almost certainly originated from the nearshore and were displaced by currents with a net offshore movement.

The smallest size at flexion for *D. s. capensis* has been recorded at 8 mm SL by Brownell (1979), a size which exceeds any of the specimens caught in this study. Larger specimens avoided capture either by active evasion or by behavioural means linked to vertical migrations or dispersal away from the sample area. The exact whereabouts of flexion and postflexion larvae remains a mystery, although the only region not sampled was the nearshore surf zone and intertidal rockpools which may be serving as nursery areas for late staged larvae and early juveniles.

Studies on the life history of *P. b. natalensis*, have been neglected in South Africa (van der Elst 1990), but a closely related species (*P. natalensis*) from the Gulf of Aden is known to spawn from late spring through summer (May to September - Druzhinin 1975). Although *P. b. natalensis* was the most abundant sparid larva during a survey of the Agulhas Current between May 1990 and February 1991 (Beckley 1993), there was no mention of seasonality. In this study no larvae were caught in spring, but winter months clearly produced significantly higher concentrations than any other time during the year. The association of larvae of this species with shelf waters (Beckley *op. cit.*), does not explain the low numbers (26) caught overall, but this species was classed as sand-associated by Tilney & Buxton (1994) and is thought to be abundant in fairly deep water (Smith & Smith 1986). The offshore distribution of larvae reflected this, with specimens coming from all stations along the transect. The inclusion of Middlebank, a major reef

structure, is not seen as strange, as the surrounding area is mainly sand and so even drift on a small scale, e.g. tidal, could explain their presence.

The observed threshold size for notochord flexion in *P. b. natalensis* (5.6 mm BL) was almost identical to that of *C. lanceps*, illustrating the close similarities which can exist during certain life history stages amongst closely related taxa. The absence of small and yolk-sac *P. b. natalensis* larvae from samples is most likely due to their absence from the sample area rather than avoidance, escapement, or extrusion, as other small sparids (1.8 mm BL) were successfully sampled with the gear during the course of this study.

Sarpa salpa has been recorded spawning in the rocky littoral zone in KZN between April and September (Joubert 1981; Van der Walt & Mann In Press), and it has been hypothesised that they are transported southwards inshore of the Agulhas Current where they utilise estuaries and shallow, sandy bays in the southern Cape as nursery or development areas. Evidence that this species does indeed spawn in the southern Cape was provided by the capture of five specimens in plankton samples. If the littoral rocky zone is also utilised as a spawning site in the region it may explain the paucity of larvae in offshore catches. Size and time of capture ranged from recently hatched (3.8 mm BL) in November to postflexion (10.5 mm BL) in May. The implications of this are that *S. salpa* most likely has an extended period during which it is capable of spawning.

Spondyliosoma emarginatum is another endemic sparid, being found between Saldanha Bay and KZN. It has been labelled a spring/summer spawner, showing activity between September and January (Penrith 1972). Its eggs are demersal, and guarded aggressively in a gravel nest constructed by the male, where they hatch after seven to ten days (Van Bruggen 1965; Beckley 1989; Buxton & Garratt 1990; van der Elst 1990). Although larvae of this species were caught in the study area, numbers were low (n = 21). The reasons for this could be two-fold. Firstly, the demersal nature of the eggs decrease the dispersal potential of the early stages such that emergent larvae may remain closely associated with the home reef and be unavailable to most gear types. Secondly, it would appear that previous researchers have collected larvae from the surf zone and lower reaches of estuaries (see Beckley 1984, 1985; Whitfield 1989a) where they were classified as marine transients. These areas could be used as nursery areas for early stages, affording protection from predators on subtidal reefs and precluding dispersal by offshore currents. The absence of larvae from all seasons except spring may reflect a short, well defined spawning season, but may

also be the result of inshore retention of larvae during the other months. The self-sustaining beach/surf zone ecosystems described by McLachlan (1990a, b) depend on a minimum of marine inputs and experience minimal loss of the component fauna and flora beyond the surf zone circulation cells. These cells are the result of interaction between shoreward moving and longshore waves which set up rip currents in a horizontal cell known as the nearshore circulation pool (McLachlan 1990a). Most of the water carried beyond the surf by the rip currents is recirculated by the breakers such that mixing between the surf zone and offshore is reduced while mixing between adjacent cells is enhanced. A mechanism such as this could conceivably be used by fish larvae to prevent offshore displacement. The high energy and reflective nature of the rocky shore in the study area differs somewhat from the high energy, exposed beaches which tend toward the dissipative extreme and where this semi-closed ecosystem is found (McLachlan 1990b). Nevertheless, a similar mechanism may be found along exposed rocky coastlines which could be exploited by intertidal and nearshore fish larvae to ensure inshore retention even during summer months when upwelling and net offshore movement of water dominates the system.

The smallest *S. emarginatum* larva (2.7 mm BL) described by Beckley (1989) had no yolk-sac remnants. Those specimens, from the Port Elizabeth region, compare well with the 2.4 mm BL larva from this site which was yolk-free. This may well reflect the demersal nature of the eggs which would preclude recently hatched larvae from near surface samples. Another similarity is the size at flexion which was 6.2 mm BL from this study and 6.0 mm BL further east Beckley (*op. cit.*). With the exception of the November 1993 samples all the rest comprised a mix of both preflexion and flexion larvae. This degree of retention can be expected when demersal eggs are the precursor to larvae, as potential for dispersal is much reduced without free floating eggs.

Six additional sparid species were caught which could not be identified further than the Family level. Of these, Species 11 was the only one which was well represented, although the majority of these larvae were caught in a single month (July 1995). The single specimen of Species 13 bore some resemblance to the illustrations of *Pachemetopon blochii* (Brownell 1979) with a few differences regarding dorsal and lateral gut pigment, and may have been the early stage of either *P. grande* or *P. aneum*. With the exception of Species 11, 3 and 12 whose presence indicated that at least partial spawning was taking place in winter, the remaining three unidentified sparids, while exhibiting a wide variation in apparent spawning seasonality, were not present in winter. Between these six species, all sample sites except the 15 nm offshore station were occupied at some stage

during the study. The wide distributional range of Species 11 offshore and to a lesser extent Species 6 could reflect a similar pattern for the adults or else fairly extensive dispersal of larvae from their point of origin which could be either offshore or inshore.

Amongst the South African sparids, *Rhabdosargus holubi* is spawned at sea and then recruits into estuaries at the post-larval stage (Whitfield 1989a) where it inhabits regions of reduced flow in order to remain in its nursery habitat. *Spondyliosoma emarginatum* is also spawned at sea but moves passively into estuaries with the flooding tide and then is returned to the marine environment on the ebb tide (Whitfield *op. cit.*). These are examples of two species which have similar habitats as larvae but ones which overlap only briefly during the early juvenile stage due to active retention in one species and passive tidal drift in the other. While southern African sparids, with the exception of *S. emarginatum*, are known to be pelagic spawners, little is known of the exact location of spawning sites and it is generally assumed that spawning takes place above any reef which provides a suitable habitat for juveniles and adults. Spawning has been observed for *C. lanceps* and *C. nufar* (Buxton 1990; Buxton & Garratt 1990) which release gametes near the surface after a complex ritual between male and female. These eggs are buoyant and prone to passive dispersal by near surface currents. It is assumed that only once larvae have the ability to regulate their position in the water column do they have any control over their dispersal. It seems unlikely that the very early stages can be assured of retention over the home reef, and this style of spawning may in fact be a type of bet hedging where overall mortality is decreased because offspring are not confined to any one area which may or may not be suitable for survival. The presence of *D. s. capensis* larvae in catches offshore from Storms River supports this early dispersal theory as adults are confined to inshore subtidal reefs (Mann 1992) well within the five and ten nm limit. This homogeneous distribution offshore of sparid larvae was also observed by Tilney *et al.* (1996) in the TNP at stations between 350 metres and 3.83 km from shore as well as over sites characterised by sand and reef substrates. The only other references to offshore distribution of sparids declare that they are rare in catches from stations over the shelf-edge and in the Agulhas Current and predominate over the inshore to mid-shelf region, with *P. b. natalensis* larvae being the most abundant (Beckley 1993, 1994).

A single *Monodactylus falciformis* flexion (4.0 mm BL) larva was captured in mid-February 1995 at a station 15 nm offshore from Storms River. This conforms well with what is known about

the genus, as flexion in *M. argenteus* larvae is reportedly between 3.7 and 4.7 mm SL (Leis & Trnski 1989). This was only the second specimen from the study area, as a single flexion larva (5.0 mm SL) was sampled by Tilney & Buxton (1994) from an inshore station in December 1990. Based on GSI values and micro- and macro-examination of gonads, *M. falciformis* is a serial spawner between October and February in Algoa Bay (Lasiak 1984). Spawning occurred close inshore but Lasiak (*op. cit.*) did not discount the possibility of offshore spawning as well. The presence of small juveniles (10 - 30 mm BL) in the upper reaches of the Sundays River estuary in late summer months (Beckley 1984) reflects a spring/early summer spawning as well. Like the congeneric *M. argenteus*, *M falciformis* spawns demersal, adhesive eggs in freshwater (Breder & Rosen 1966 in Leis & Trnski *op. cit.*; Neira 1998) and pelagic eggs in seawater. The paucity of these larvae in our samples may reflect a function of inshore retention around river mouths and their recruitment into estuaries for the duration of the juvenile phase.

A preflexion yolk-sac larva of 2.7 mm BL, identified as *Seriola lalandi* was caught off Middlebank towards the end of April 1996. Published material on the spawning season of this fish could not be found except for a mention in van der Elst (1990) that spawning has been recorded off the KZN coast, with juveniles occurring as far south as False Bay. Given their circumglobal distribution, mainly in subtropical and temperate waters (Smith-Vaniz 1986) spawning is likely to occur over much of this range. According to unpublished data from the SFRI in Cape Town, yellowtail may spawn anywhere between southern KZN and Dassen Island over an extended period from September to June, with peaks in December and January. During the Cape Egg and Larval Program (CELP) between August 1977 and August 1978, larvae were found between five and thirty nm offshore between Cape Point and Mossel Bay on a regular basis but in low concentrations. Adults constantly undertake inshore/offshore migrations which are related to water movement and to a lesser extent baitfish distribution, and are capable of spawning at any time if conditions are right (Andrew Penney, Pisces Research and Management Consultants, Pers. Comm.).

Trachurus trachurus capensis larvae were caught all year round from 1950 to 1967, being least abundant in July and most abundant in October (Haigh 1972b). On a seasonal basis, spring months yielded the most. These data came from samples off Fisheries research vessels and most likely encompassed most of the distributional range in southern Africa. On a smaller scale, O'Toole

(1977b) and Olivar (1987a, 1990) noted a peak spawning period in summer/autumn off Namibia, and Shelton (1986) recorded a peak later in the year over winter/spring in inshore waters of the southern Benguela system which coincided with periods of low upwelling activity. This concurs with the early work of Gilchrist & Hunter (1919) who described eggs of this species from the Cape of Good Hope which had been caught in August and September, although there are also records of eggs in December (Gilchrist 1903) and March (King *et al.* 1977) from False Bay. Over the eastern Agulhas Bank, Hecht (1990) recorded maximum GSI's from adult fish in June and November, stating that spawned eggs and larvae recruit into the numerous embayments along the south coast, while further west the months of August and February were found to be the time of peak reproductive activity (Naish 1990). In this study, catches of larvae were sporadic but the clear seasonal pattern mentioned earlier was observed with larvae most prominent in the winter months from June to August. This is in partial agreement with the pattern described by Naish (*op. cit.*) for the western Agulhas Bank. Their absence in February samples could be explained by Hecht's (*op. cit.*) proposal that they were in the sheltered embayments further to the west at Plettenberg Bay or the east in St. Francis Bay. A pattern similar to this was observed by Buxton, Smale, Wallace & Cockroft (1984) where *T. t. capensis* juveniles less than one year old were found to be abundant in Plettenberg Bay and Algoa Bay.

Larvae of *T. t. capensis* were generally well represented in samples from both inshore and offshore stations during this survey. Their homogeneous distribution along the transect is a good indication of widespread adult distribution, pelagic spawning and subsequent dispersal of propagules. This widespread distribution was not observed in a previous study (Tilney & Buxton 1994) where only a few specimens (n = 32) were caught from inshore stations within the TNP. At around the same time, stations along an offshore transect at Algoa Bay and Plettenberg Bay over the shelf-edge between 45 and 90 km offshore produced the highest concentrations (Beckley 1994). It is possible that spawning in this species took place over the shelf-edge area during those years, but subsequently during this study period spawning was either more widespread, incorporating inshore sites, or it had moved closer to the shore altogether. The sampling of the 15 nm station in summer months when spawning in the species is at an ebb and the fact that no stations extended further than the mid-shelf region meant that the distribution of larvae over the shelf-edge could not be determined. On the west coast of South Africa and off northern Namibia, *T. t. capensis* larvae displayed a widespread

horizontal distribution extending from close inshore out to the shelf-edge (Olivar & Rubiés 1983; Shelton 1986; Olivar 1990).

Other studies on *T. t. capensis* larvae displayed similar sizes for yolk-sac absorption and flexion as were observed here. The smallest larvae sampled by Haigh (1972b) measured 2.45 mm SL and had already absorbed all the yolk, while according to her illustrations, flexion was around 5.8 mm SL. In this study, yolk absorption was completed by 2.2 mm BL and flexion was evident by 5.7 mm BL. While this points to a degree of control over developmental rates over much of its distribution, Olivar & Fortuño (1991) fixed flexion at a slightly larger size between 6.0 and 8.0 mm SL for larvae sampled in Namibian waters.

The identification of the specimens tentatively classified as *Cheilodactylus fasciatus*, an endemic found between the Cunene River and KZN, was based on the description by Brownell (1979) who himself expressed a certain amount of reservation as to its accuracy, stating that the larvae may also have been those of *Chirodactylus brachydactylus*. In this study, larvae which were similar in appearance to Brownell's *C. fasciatus* except for variation in pigment patterns and a discrepancy with pre- and post-anal myomere counts were tentatively thought to be *C. pixi*, but had to be labelled Species 1 until positive identification is possible. Species 2 could be either *C. brachdactylus* or *Chirodactylus grandis*. Eggs which were attributed to *C. fasciatus* were caught sporadically between January and September in Table Bay by Gilchrist & Hunter (1919) and from February to September (Brownell 1979) around the Cape Peninsula over half a century later. All cheilodactylid species caught in this study were present in winter between July and August, with a few Species 1 larvae present sporadically in spring and autumn months. The spawning season for *C. brachydactylus*, which is endemic between Walvis Bay and Delagoa Bay, has been described as early summer (van der Elst 1990), a pattern which Species 1 appears to follow in this region. The absence of Species 1 larvae from the 15 nm station may not be due to the absence of nearby spawning adults but because the spawning period appears to exclude the summer months when the 15 nm station was sampled. Adult *C. brachydactylus* are commonly found along the rocky shore of southern Africa, with specimens being found as deep as 240 metres off KZN (Smith 1986c), so the presence of cheilodactylid larvae at 10 nm in water up to 102 metres deep was not considered unusual even though evidence of reef over the site was lacking. Nevertheless, even in the absence of reef, larvae could easily have been transported offshore from any site inshore where subtidal reef abounds. No information from other parts of the

country is available, but *C. fasciatus* larvae that were caught by Brownell (1979) around the Cape Peninsula were close inshore.

Bruce (1989b) quotes a size range of 5.5 - 7.5 mm BL for the onset of flexion in cheilodactylids, while Brownell (1979) only observed flexion in *C. fasciatus* larvae > 7.5 mm SL. He also measures the size at hatching at between 2.5 and 3.3 mm SL for *C. fasciatus*, which compares well with the observed 3.4 mm BL yolk-sac Species 1 larvae in this study. Although a wide size range of preflexion larvae was caught during the study, the absence of flexion stages may be the result of a restricted sampling regime and a more diffuse distribution during these later developmental stages.

Adults of the endemic mullet species *Liza richardsonii* have been recorded from the study area by Burger (1990), and its larvae as well as those of *Mugil cephalus* have been described (Brownell 1979; Cambray & Bok 1989). The identification of the third species caught during this study was complicated by poor representation, a host of possibilities when considering the distributional range of the many mullet species, and the lack of any descriptions of early life history stages other than the two previously mentioned. According to the distributional records (Smith & Smith 1986) there are five species of mullet found in the study region. Larvae of both previously described species were encountered during this study, with *L. richardsonii* being represented by single specimens in November 1993 and 1995. Two postflexion *M. cephalus* larvae were caught over Middlebank in November 1994. Gilchrist & Hunter (1919) unknowingly sampled the eggs and larvae of *L. richardsonii* from False Bay which they identified as *Merluccius capensis*, but there was no indication of when during the year they were caught. Brownell (*op. cit.*) recorded their eggs in the waters surrounding the Cape Peninsula from July to October although his identification has been questioned by Cambray & Bok (*op. cit.*) based on oil globule patterns on the egg, egg diameter, size of newly hatched larvae, shape of the yolk-sac, pigmentation of the finfold, absence of xanthophyll, and number of myomeres in early free embryos. In addition, the spawning season along the south-east coast (Lasiak 1983) has been reported as being in summer, and not winter/spring, which coincides with the presence of larvae in the study area during November. Eggs identified as *M. cephalus* were collected by Brownell (*op. cit.*) from July to October on both sides of the Cape Peninsula. This compares well with data from this study as the postflexion larvae caught in November 1994 would have been spawned in early October. A single preflexion Species 3 larva (3.8 mm BL) was caught 15 nm offshore in February 1995. Based on egg incubation times

for *L. richardsonii* (Bok 1989) of between 46 and 60 hours and developmental times in Cambray & Bok (*op. cit.*) and Brownell (*op. cit.*) of between seven and ten days to reach approximately 3.8 mm BL, this larva was spawned near the beginning of the month. Based on distributional records (Smith & Smith 1986), this larva could have been *Liza dumerili*, *L. tricuspidens* or *Valamugil buchanani*.

Champsodon capensis is a small pelagic shoaling fish found in the northern Indian Ocean and between the Cape and Durban (Heemstra 1986b) in deep water. The presence of a large postflexion larva close inshore may be mostly due to passive drift away from the spawning grounds. Adults aggregate near the surface at night and are prone to being washed ashore in rough conditions (Heemstra *op. cit.*), and a similar behaviour may occur in postflexion larvae. The presence of larvae in cathces from the Arabian Sea (Fursa 1974) pointed to a year round spawning habit. No information on spawning habits in South African waters is available, but based on its capture time in October 1995 a rough estimate would place time of emergence at around late autumn earlier that year.

The lack of larval descriptions also hampered the identification of blenny species. The two which were identified were based on descriptions by Olivar (1986) for *P. pilicornis* and De Leo, Catalano & Parrinello (1976 in Olivar & Fortuño 1991) for *Scartella emarginata*. A total of six blenny species were separated from plankton samples, but only four, including *P. pilicornis*, have been documented in previous collections of adult fish from the region (although *O. woodi* has not yet been recorded it is likely that it is present). This most likely means that adults of *S. emarginata* plus one of the other species which was caught infrequently (either Species 3 or 6) are not found within the study area, but that their eggs and larvae drift through the area on occasion.

Parablennius pilicornis spawns during autumn off Namibia (Olivar 1986, 1990) when the process of upwelling occurs less frequently and warm Angolan water penetrates southwards. Adults spawn inshore, and like the rest of the Blenniidae probably lay demersal eggs which adhere to a substrate or each other by filaments (Matarese, Watson & Stevens 1984) and which are guarded either by both or a single parent (Thompson & Bennett 1953; Shiogaki 1982). Incubation in this group may be anywhere from six to seventy days. Larvae were present for most of the year during the study, although the winter/spring period proved most productive. This may well be evidence of an attempt to maximise output before the onset of the upwelling season along the east

coast, much like the strategy employed along the coast of Namibia. Adults of *P. pilicornis* are widely distributed, but in southern African waters have only been reported from Knysna to Sodwana Bay (Springer 1986) and off northern Namibia (Olivar 1986, 1990). There is no known reference to the depth distribution of larvae along the east coast, but they have been found from close inshore out to the continental shelf and slope of Namibia (Olivar 1986) in 200 metres of water. Small larvae seem to be restricted to the inshore region with larger larvae being found offshore as a result of displacement by Eckman transport. It appears therefore that the distribution pattern observed in this study may follow a similar pattern to that observed off Namibia, although no samples were taken as far out as the shelf break. While blenniid larvae were found to be significantly more abundant at inshore stations in the TNP by Tilney *et al.* (1996), where concentrations 0.35 km from shore superseded those found at both 1.26 and 3.83 km sites, their larvae were equally distributed over areas defined by reef or sand substrate. The different scale of inshore/offshore, however, makes a direct comparison with this study difficult.

A single *Scartella emarginata* postflexion larva (17.36 mm BL) was caught towards the end of the upwelling season in March 1994 on Middlebank. According to van der Elst (1990) adults are exclusive inhabitants of the intertidal zone and rockpools, and breeding may occur at any time during the year. The eggs are benthic and guarded by the males for the six month incubation period. Based on this, it would appear that the larva in question emerged from an egg spawned in October 1993. The paucity of this species in plankton samples could well be a function of retention in the intertidal zone and rockpools, or of adult distribution patterns.

Of the four remaining blenny species, Species 3 and Species 6 were scarce in catches, but both appeared to make use of conditions in winter/spring months, avoiding summer as was the case in those blenny species already discussed. While the second most abundant blenniid, Species 4, was present in all seasons except autumn, peak spawning again appeared to take place at such a time to ensure that larvae emerged in winter and spring before upwelling. The situation for Species 5 was somewhat different, with maximum concentrations being found in the middle of the spring/summer upwelling season. It could be that retention inshore of this species is not a priority and maximum spawning takes place at such a time that emergent larvae could well be displaced great distances if trapped in a cell of upwelled water.

Blennies hatch from small eggs attached to the substrate (Munro 1955) at between 2.0 and 3.0 mm BL. Yolk absorption is thought to be a fast process, as the smallest *P. pilicornis* specimen examined by Olivar (1986) measured just 2.4 mm NL and displayed no evidence of yolk-sac remnants. This is confirmed here as the smallest larvae in these samples (1.9 - 2.8 mm BL) were also devoid of yolk-sacs. Flexion for the Blenniini (the Tribe to which *P. pilicornis* belongs) is between 4.0 and 4.4 mm (Watson 1983), however, Olivar (*op. cit.*) puts it later between 5.0 and 6.0 mm SL which is more in accordance with the observed 5.5 mm BL in this study. The absence of large flexion and postflexion *P. pilicornis* larvae, the disappearance of Species 4 larvae from the samples after 8.5 mm BL, and the lack of flexion larvae amongst Species 5 catches may be as a result of avoidance due to increased motility, but could also indicate early settlement behaviour prior to metamorphosis, meaning that these species have a reduced pelagic component to their life cycle. This applies particularly to Species 4 where very small larvae were also absent, perhaps indicating an association with the substrate for a few days immediately after hatching before the larvae enter the pelagic environment.

Two Ammodytidae species are found in our waters (Heemstra 1986c) with the one, *Bleekeria renniei* being classified as rare and extending only as far south as Port Alfred. The second species, *Gymnammodytes capensis*, which is an endemic found between Angola and Delagoa Bay, is referred to as plentiful along the Cape south coast where it is found over sandy bottoms in littoral and neritic waters. Prior to this, their larvae had not been described but comparison of the two preflexion larvae caught in this study with sandlance larvae illustrations in Leis & Trnski (1989) and (Stevens, Matarese & Watson 1984) confirmed them as belonging to this Family. The low numbers in samples could be as a result of the eggs being demersal and adhesive in clumps on sandy substrates and the close affinity of hatched larvae with the bottom. A preliminary estimate of spawning seasons is risky when only two larvae were captured at different times as it could either indicate a prolonged season from December through to April or two short, well defined spawning events.

The early life history of dragonets is characterised by an extended pelagic phase with eggs, larvae and post-larvae being found in the plankton (Fricke 1986). The first reference to the seasonality of the endemic *P. costatus* was by Gilchrist (1904) who collected eggs (species XVIII. page 143) in False Bay in November 1903. A single egg which appeared similar had previously

been caught 25 nm off Cape Point in September of that year. Later, Gilchrist & Hunter (1919) sampled eggs in Table Bay between September and January, and Brownell (1979) discovered them to be regular components of plankton catches from March to November in the same region, leading him to conclude that they spawn all year round with possible peaks in March/April (early autumn) and September to November (spring). Later work in the south-east Atlantic (Olivar 1987b) confirmed this when samples from all year round contained *P. costatus* eggs and larvae. Along the south-east coast during this study, larvae were also caught all year round except during May and June, with spring and winter being the most productive seasons in that order. While May was sampled twice during the three year period, June was only sampled once (1995) so the absence of larvae from these months should not be taken to mean they were not present in the area, just that patchiness precluded their capture. Surprisingly, only two specimens of this species were caught in the previous survey by Tilney & Buxton (1994) compared to the 429 (3.8% of total catch) in this study. The absence of a distinct spawning season for *P. costatus* in the study area means that their absence from the 15 nm station may be due to larval patchiness and insufficient sampling, as adult fish are also found in deep water from 55 to 400 metres (Fricke 1986). This widespread distributional pattern of adult fish appears to carry over into the early life history stages. Callionymid larvae, presumed to be mostly *P. costatus*, were captured at stations all over the shelf and slope off Algoa Bay and Plettenberg Bay in January 1992 (Beckley 1994), and were predominant in catches between 130 and 500 metres in the southern Benguela system (Olivar & Fortuño 1991), reinforcing the extensive offshore distribution of early life history stages observed for the species in this study.

The size class of *P. costatus* larvae possessing yolk-sacs in this study compares well with the general size at hatching for the family at around 1.1 to 1.3 mm SL (Leis & Rennis 1983). Olivar (1987a, b) stated that flexion in *P. costatus* in the Benguela system commenced around 5.0 mm SL and reached completion at 5.5 mm SL, while Leis and Rennis (*op. cit.*) observed it as early as 2.3 to 3.4 mm in Indo-Pacific callionymid species. The onset of flexion observed in this study (5.2 mm BL) agrees with the west coast data, but size at completion (> 8.0 mm BL) appears to be considerably larger. The existence of large well developed postflexion larvae in the plankton together with smaller stages suggests a prolonging of the pelagic phase prior to settlement. A plausible reason for this could be predator avoidance, as *P. costatus* has been recorded as an important prey item in several demersal species off the south coast of South Africa, namely *Chelidonichthys capensis*, *Chelidonichthys queketti*, *C. zanzibarensis*, *G. gonorhynchus*, and

Helicolenus dactylopterus (Meyer & Smale 1991; M°Phail 1997), and the skates *Raja miraletus*, *R. alba*, *R.* cf. *clavata*, *R. pullopunctata*, *R. wallacei* and *Cruriraja parcomaculata* (Smale & Cowley 1992).

In a review on gobioid fishes by Ruple (1984) it was stated that less than 5% of the approximately 2 000 species in this group of fishes have descriptions of their early life history stages. In the previous ichthyoplankton survey of the region (Tilney & Buxton 1994), three species of goby larvae were sampled, compared with four in the present study. Three adult species, all *Caffrogobius* spp., were recorded by Burger (1990) which led Tilney & Buxton (*op. cit.*) to assume they were the three larval species, although it was not possible to ascribe each larva to a specific adult type. According to Hoese (1986) there are roughly 107 goby species in South African waters. The adult distributional ranges of nine of these overlap the study area, with an additional species (*Glossogbius callidus*) being previously recorded as far south as Algoa Bay. The identification of the goby larvae to species level is therefore not possible until larger specimens with complete fin element counts can be caught and related to the smaller sizes.

The eggs of the Gobiidae are known to be benthic and adhesive, many with filamentous strands for attachment to the substrate, and may be guarded by either one of the adults (Leis & Rennis 1983; Ruple 1984). In southern African waters, O'Toole (1978b) described the larvae of *Sufflogobius bibarbatus* off Namibia, Melville-Smith (1978) described *Psammogobius knysnaensis* from the Swartkops Estuary, and Olivar (1989) dealt with *Lesueurigobius sanzoi* in the Benguela system. Apart from these, the gobiid ichthyoplankton fauna have not been the subject of much attention and descriptions of early life history stages are sorely lacking. Two of the three species sampled in this study were absent from catches in summer, with the third species exhibiting its lowest concentrations at that time. Autumn and winter were the peak spawning times for these species, a fact noted for *L. sanzoi* along the Namibian coast. *Sufflogobius bibarbatus* appears to be the only exception, with larvae occurring most frequently in spring/summer during intense upwelling activity (Olivar & Fortuño 1991).

Gobiid larvae emerge from their benthic eggs anywhere between 1.7 and 4.4 mm SL depending on the species (Leis & Rennis 1983). All three goby species from this study appeared to fit in at the lower end if this scale. In comparison with Indo-Pacific species which initiate flexion between 2.7 and 3.8 mm SL (Leis & Rennis *op. cit.*), Species 1 was a late developer but conforms well with two species from the Benguela system, namely *L. sanzoi* and *S. bibarbatus* which attain flexion

between 4.0 and 5.0 mm SL (Olivar 1989; O'Toole 1978b; Olivar & Fortuño 1991). Species 3 appeared to reach flexion at a smaller size. The absence of postflexion Species 1 and flexion Species 2 larvae suggests a dispersion of the later stages away from the sample area, perhaps back down to the substrate. On two occasions, Species 2 larvae were observed in the gut of arrow worms (chaetognaths), indicating the possibility of predation pressure leading to an avoidance of the pelagic environment. The smaller size at flexion for Species 3 and the presence of all developmental stages in catches, may indicate an advanced swimming and predator avoidance capability which allows them to remain in the plankton for a longer period prior to settlement.

The first account of early development in *Thyrsites atun* came from De Jager (1955) after he successfully fertilised eggs obtained from a ripe female with sperm from a ripe running male from the same trawl off St. Helena in October 1950. An earlier spawning season was detected by Nepgen (1979) also from the south-west Cape where peak activity was from March to August. Further east and northwards the consensus appears to be for a period from late winter to spring (van der Elst 1990), with ripe females being observed in KZN at that time (Marc Griffiths, SFRI. Pers. Comm.). Catches of larvae during this study were exclusively in winter and only on two occasions. The chances are that these larvae were carried into the reserve from the nearby snoek banks and their capture was a chance encounter. With this limited data, it was not possible to determine the exact spawning season for *T. atun* in the region. Based on initial accounts of supposed spawning seasons (see above) it appeared that snoek larvae were absent from late spring through summer. It was first thought that this may have something to do with avoiding upwelling activity during this period. However, during research voyages between November 1979 and April 1986 in the Benguela system, larvae of this species were most abundant when colder upwelled water was present over the continental shelf (Olivar & Fortuño 1991), although this was during winter months. The absence of larvae during spring/summer may, however, be the result of more generalised seasonal trends in water temperature or productivity.

Only ten *Lepidopus caudatus* larvae were caught. April and August 1995 produced one yolk-sac (4.0 mm BL) and one flexion (13.7 mm BL) respectively, with eight (5.6 - 7.1 mm BL) being caught in October 1995. Eggs and larvae of this species were present in low numbers for most of the year in the Benguela system, and in months from all seasons (also in low numbers) except summer in this study. Adult fish are benthopelagic, in waters down to 400 metres (Nakamura

1986), and in New Zealand waters they spawn over the mid- to outer-shelf in 50 to 200 metres of water (Robertson 1980). If spawning along the south-east coast of South Africa follows a similar pattern, the distance offshore would be considerable and this may well preclude high concentrations of the early stages in shallower inshore waters where most of this sampling was carried out. In addition, once eggs of this species have hatched near the surface, the larvae sink rapidly (Robertson *op. cit.*) which would have taken them out of the reach of the main sampling gear (bongo's) operating at a maximum depth of 18.5 metres. The New Zealand spawning season is also protracted, with adults starting to congregate in spring and peak spawning following in summer and autumn in most places.

Scomber japonicus, which is one of the most important commercial species in the west-coast purse-seine fishery, spawns in winter from June to mid-August (Baird 1977), with the period from January to May proving the least active. This observation was based on fish sampled at processing plants along west coast from 1969-1973 and so the exact origin of these fish was not always clear, but it is assumed that they were predominantly from the southern Benguela region. In the waters off Namibia between Walvis Bay and Lüderitz larvae were absent, but eggs were caught during the autumn months (Olivar & Fortuño 1991). The spawning period for this species from the Canary Islands extends from November to March (Lorenzo & Pajuelo (1996), i.e. winter, which is in agreement with other studies on this species off north-west Africa. During this study, larvae appeared in catches in August (twice) and October (once), i.e. late winter/spring, conforming to the seasonal pattern already reported.

An egg identified as belonging to the endemic *Arnoglossus capensis* was caught in False Bay in November 1903 (Gilchrist 1904), with subsequent catches coming from the nearby Table Bay during the months of March and October (Gilchrist & Hunter 1919). According to Brownell (1979), year-round spawning takes place in False Bay with a peak on the western side of the Cape Peninsula between March and June. A single *A. capensis* preflexion larvae (3.2 mm BL) was caught five nm off Storms River in August 1995. This is well within the adult distributional range which is on sand and shell bottoms from 1 to 110 metres (Hensley 1986). The absence of further specimens from samples could not be explained.

Although the distributional range and habitat of *Cynoglossus capensis* and *C. zanzibarensis* overlap, catches of the former were rare in the study area while the latter featured prominently. The reverse was thought to occur by Tilney & Buxton (1994) but this would appear to have been due to incorrect identification. Gilchrist & Hunter (1919) first recorded the presence of the endemic *C. capensis* in Table Bay in September and December when they identified eggs very similar in appearance to *Arnoglossus* sp. and designated them Species XXIV. Brownell (1979) sampled *C. capensis* eggs in False Bay and to the west throughout the year with no apparent seasonal trends, a pattern also observed for eggs and larvae along the west coast by Olivar & Fortuño (1991). Only six *C. capensis* larvae were identified during this work from different times of the year and from different sample sites. These data were not sufficient to shed light on any possible trends in reproductive seasonality.

Cynoglossus zanzibarensis on the other hand was abundant in samples (2.99% of total catch) and was present in catches all year round. There are no references to this species' early life history or its reproductive habits in our waters. Heemstra (1986d) states that the adults are widely distributed and most definitely sand-associated. The presence of larvae over the Middlebank reef, however, shows that the early life history stages are not necessarily retained over the spawning sites. Size at hatching in the Cynoglossidae has been documented from anywhere between 1.2 and 3.5 mm BL, with newly hatched larvae in possession of a large yolk-sac (Fujita, Kitajima & Hayashida 1986), which may explain the yolk-sac remnants present on *C. zanzibarensis* larvae some time after hatching. Leis & Trnski (1989) report flexion taking place between 6.6 and 9.8 mm BL for Indo-Pacific members of the family and Brownell (1979) shows this stage to be attained by 9.9 mm SL, slightly larger than the 7.8 mm BL observed in this study. The co-occurrence of most developmental stages in many catches points to a prolonged spawning period, retention and a long planktonic existence in the early life history period.

Spring was the peak season for larval abundance, followed by summer and autumn, for the endemic *Austroglossus pectoralis* in the study area. This fish is the most important commercial flatfish species off South Africa (Heemstra & Gon 1986). Unpublished data from the SFRI in Cape Town has shown that peak reproductive activity is between April and October (Frances Le Clus. SFRI, Pers. Comm.). Evidence from captive specimens pointed to a year round spawning capability (Le Clus, Henig, Melo & Boyd 1994) which supported earlier field observations by Zoutendyk (1974), Hecht (1976) and Payne (1986 in Le Clus *et al.* 1994). While adults are found

in waters between 10 and 120 metres (Heemstra & Gon *op. cit.*), they appear to spawn between Cape Agulhas and Port Alfred in waters between 50 and 108 metres over a mud or sandy seabed (Le Clus *et al. op. cit.*). Eggs are probably released off the bottom above the nepheloid layer which covers mud patches. The closely related *A. microlepis*, also appears to have a prolonged spawning season, from March to November, around the Cape Peninsula (Brownell 1979). Off Namibia, *A. microlepis* larvae were sampled between September and January in upwelling centres, although no sampling was carried out for the rest of the year (February to August) so the duration of spawning could not be ascertained (O'Toole 1977a). Olivar & Fortuño (1991) also recorded *A. microlepis* larvae mostly during periods of intense upwelling along the coast of Namibia. The spring and summer peaks in larval concentration for *A. pectoralis* in this study could also be a reflection of a preference for spawning during the upwelling season on the east coast. The absence of larvae from 15 nm sites is not easily explained as they are known to spawn at that time (summer) and depth. It is more likely a case of patchiness than absence from the region.

Prior to this study, early development in *A. pectoralis* had not been described. Larvae belonging to the family Soleidae hatch anywhere between 1.7 and 4.1 mm BL (Brownell 1979), with *A. microlepis* emerging at just < 2.7 mm SL. *Austroglossus pectoralis* hatches at a smaller size than its west coast con-generic and, like *C. zanzibarensis*, appears to retain the yolk-sac for a reasonable period (up to 2.9 mm BL). O'Toole (1977a) reports the commencement of flexion in *A. microlepis* to be at 5.2 to 5.5 mm SL while the soles as a group may attain this threshold anywhere between 3.2 and 9.4 mm BL (Balkarishnan & Devi 1974; Leis & Trnski 1989). While *A. pectoralis* conforms to the general pattern for the Soleidae, flexion is initiated at a considerably smaller size (3.5 - 3.8 mm BL - see Chapter 4) than for *A. microlepis*. Settlement most likely occurs before the postflexion stage is attained as none of these late stages were caught in the samples.

The adults of *Heteromycteris capensis*, which are endemic between Walvis Bay and Maputo, are commonly found in shallow waters (1 - 25 m) and the juveniles frequent sandy estuaries (Heemstra & Gon 1986). No mention of the whereabouts of larvae is given, but they may be close inshore near to estuary mouths and hence unavailable to offshore sampling programs. Eggs of this species (then known as *Achirus capensis*) were procured from ripe females in False Bay in the months of November and December (Gilchrist 1903), but fertilisation from ripe male gonad tissue was not successful. A fertilised egg caught around the same time did hatch out (named Species V) and it was tentatively suggested and later confirmed (Brownell 1979) that this was the larva of *H.*

capensis. Eggs of this species were present all year round, except in August, in False Bay (Brownell 1979), but spring and summer (October to February) were the seasons in which the heaviest spawning took place. Interestingly, Brownell (*op. cit.*) caught no eggs on the Atlantic side of the Peninsula, and no larvae were ever caught in the Benguela system by Olivar & Fortuño (1991) between November 1979 and April 1986, even though its known distributional range is from Walvis Bay to Maputo (Heemstra & Gon *op. cit.*). Larvae and reproductively active adults of *H. capensis* were found to be present during most months of the year in the nearshore zone of Algoa Bay (Lasiak 1982; Beckley 1986), but Melville-Smith (1981) only found larvae in the lower reaches of the Kromme River estaury between January and November. During this study, larvae were also found in samples all year round, but never in any great numbers, with spring and summer months proving to be most productive, conforming to what has previously been discovered about adult spawning habits.

According to Brownell (1979) flexion in *H. capensis* from False Bay had not yet started at 3.6 mm SL but was found to be complete by 6.2 mm SL. So while the postflexion stage is attained at a smaller size to those larvae from this study, the size at the onset of flexion is still unknown. The absence of postflexion larvae from the sampled area could be due to early settlement, a phenomenon which has previously been recorded in captive specimens after about one month post-hatch at 6.6 mm SL (Brownell 1979).

Three larvae were tentatively identified as *Monochirus ocellatus*. In southern Africa this species is known only from the eastern Atlantic and KZN and is considered rare (Heemstra & Gon 1986). Olivar & Fortuño (1991) sampled larvae from near the Cunene River on the Namibia/Angola border during April of 1981 and 1986 when upwelling was least active. Similarly, all three larvae from this study were caught in April, a time when upwelling along this part of the coast is rare. Identification of these three specimens was based on illustrations which were originally done by Palomera & Rubiés (1977 in Olivar & Fortuño *op. cit.*).

A single flexion *Solea bleekeri* larva (4.2 mm BL) was caught over Middlebank in March 1996. Adults, which are endemic between False Bay and Maputo, are thought to spawn both at sea and in estuaries (Wallace 1975; Melville-Smith 1978; Cyrus 1991) with juveniles being frequently found on shallow sand banks. Eggs collected by Gilchrist (1904) during November in False Bay were labelled as Species XVII and considered by Brownell (1979) to be either *S. bleekeri* or *S. fulvomarginata*. In more recent times Brownell (*op. cit.*) caught a number of eggs in False Bay

during November and February and reared the hatched larvae to 16 days. He tentatively identified them as *S. fulvomarginata* based on myomere counts but did not rule out the possibility of *S. bleekeri* due to poor fixation of specimens. In KZN, this species is thought to spawn in the St. Lucia Estuary from June to August (Wallace *op. cit.*) or September to November (Cyrus *op. cit.*). Although the latter author did find ripe fish from as early as July, ripe running fish were evident only later. Further south in the Swartkops Estuary they spawn from October to February (Melville-Smith *op. cit.*), and in Algoa Bay they spawn in summer and winter with larvae being most abundant in summer (Beckley 1986). This conforms nicely with the larva found in this study. Larvae may be retained in the estuaries, hence catches of them are rare, but juveniles are supposedly dispersed by ocean currents (van der Elst 1990). The presence of eggs in False Bay which were thought to possibly belong to *S. bleekeri* (see above) show that there is a possibility that at least in the southern Cape there is a tendency for using the inshore area as well as estuaries as spawning grounds.

The distributional range of *Synaptura kleini* includes the eastern Atlantic around our coast up to Durban (Heemstra & Gon 1986), but as yet eggs and larvae have not been captured west of False Bay. It has been described as a shallow water species which may exhibit inshore retention of eggs and larvae, thereby making them unavailable to plankton sampling during most research voyages. A single egg was caught in False Bay in December 1902 and the hatched larva identified as species VII (Gilchrist 1904), later *Solea capensis* (Gilchrist 1916) and finally *S. kleini* (Brownell 1979). Brownell (*op. cit.*) also collected eggs from False Bay between October and April. The two larvae identified as *S. kleini* during this study were caught within this period. A yolk-sac larva (2.7 mm BL) was caught at the start of the spawning season in October 1995, and a flexion larva (6.5 mm BL) was sampled in April 1995. Back calculating for the flexion specimen from reared larvae of the same size (Brownell *op. cit.*, p45. Fig. 52) meant that this larva emerged sometime in the last week of April, i.e. towards the end of the proposed spawning season.

In a generalised statement, Champalbert & Koutsikopoulos (1995) refer to the majority of flatfishes as offshore spawners whose larvae and early juveniles are transported inshore to nursery areas. Although passive mechanisms cannot be ruled out, evidence gathered for Dover sole (*Solea solea*) points to vertical migrations to take advantage of tidal currents for horizontal displacement inshore, and once there for retention (Koutsikopoulos, Fortier &

Gagné 1991). In the northern region of the Bay of Biscay, spawning occurs from 40 to 80 km offshore of the nursery grounds which implies considerable distances are covered by the time the juvenile phase is attained (Koutsikopoulos & Lacroix 1992; Koutsikopoulos, Dorel & Desaunay 1995). Similar findings were obtained in studies on North Sea plaice (*Pleuronectes platessa*) which spawn offshore 30 to 60 km away from their surf zone and estuary nursery areas in the southern North Sea and eastern English Channel (Harding, Nichols & Tungate 1978; Rijnsdorp *et al.* 1985). Larvae then utilise tidal currents to move great distances inshore and remain there.

Little is known of the larval transport from spawning areas of flatfish species found in southern African waters. For many, however, it would appear that spawning takes place both offshore and close inshore. Spawning in *A. microlepis* is confined to within 30 km from the shore along the West Coast (O'Toole 1977a) and eggs can be found close inshore around Table Bay and False Bay (Brownell 1979). Although only a few larvae of the closely related *A. pectoralis* were caught, they were widely distributed from inshore at Middlebank to 10 nm offshore. Egg identification was not possible, but recently hatched larvae both inshore and offshore make it likely that spawning is not a result of an adult migration to a confined area but is instead widespread over their distributional range. Data for *H. capensis* is sparse. although Brownell (*op. cit.*) did collect eggs close inshore in False Bay. Only four larvae were caught over this eight month period, but they came from stations at Middlebank and 10 nm. If spawning does take place at considerable distances from shore then a mechanism of transport similar to that for *P. platessa* may be utilised, as *H. capensis* is also known to use estuaries as post-larval and juvenile nursery areas (Whitfield 1994). Eggs and larvae of *Cynoglossus capensis* have been collected both relatively close to shore (Brownell 1979) and further afield in the southern Benguela (Olivar & Fortuño 1991) in water 120 to 360 metres deep. Nothing on the distribution of *C. zanzibarensis* larvae has been published, but they too appear to have a widespread range, being found at all sites, from Middlebank to 15 nm in this study. The two *Cynoglossus* species exhibited a wide ranging horizontal distribution off Algoa Bay and Plettenberg Bay (Beckley 1994) but were most abundant over the inner shelf at stations 20 and 45 km offshore from Algoa Bay and < 1 km from shore at Plettenberg Bay. Unfortunately Beckley (*op. cit.*) does not differentiate between the two species so specific patterns are not clear. Similarly she declares that soleid larvae were found in low concentrations at inshore stations along both transects, but does not specify which species were involved.

The squid, *Loligo vulgaris reynaudii*, has the ability to breed at any time of the year between False Bay in the west and Port Alfred in the east (Augustyn, Lipinski & Sauer 1992). There are, however, two recognised peaks in activity, a major one from September to December and a lesser one from March to July (Augustyn, Lipinski, Sauer, Roberts & Mitchell-Innes 1994) with the majority of spawning taking place between Plettenberg Bay and Algoa Bay (Wallace, Kok, Buxton & Bennett 1984; Augustyn 1990; Sauer, Smale & Lipinski 1992). Spawning sites have been identified in the study area, with a site just off Bloukrans River being the most frequently used (Sauer 1995). Catches of squid para-larvae were sporadic during August 1993 (13), October 1995 (11) and April 1996 (5) for an overall total of 29. The possible reasons for these low numbers are three-fold. Firstly, although spawning does occur within the study area it is limited and sporadic (Sauer *op. cit.*) and hence larval presence and numbers would follow suit. Secondly, due to the passive nature of the early planktonic phase in squid and their poor swimming abilities during this period (Arkhipkin & Fedulov 1986), which can be between two and three months, their numbers are prone to dilution and wide ranging dispersal by currents away from the spawning ground. Thirdly, para-larvae appear to stay close to the bottom during the day (Warwick Sauer, DIFS, Rhodes University, Pers. Com.) out of range of conventional sample gear types. Whether the para-larvae caught even originate from within the study area is debatable as their poor swimming abilities could mean that they were transported to the study area from distant spawning grounds.

Temporal Distribution

The temporal distributional patterns of larvae for a number of fish species agree in part or totally with previously observed spawning periods determined either from plankton surveys or studies on gonad maturation in adult fish. In these cases the use of GSI indices and gonad states to delimit the spawning periodicity was justified. Included among those whose presence as larvae in the study area was compatible with recorded spawning seasons in their entirety were *E. whiteheadi*, *L. hectoris*, *S. barnardi*, *M. capensis*, *Chelidonichthys capensis*, *P. olivaceum*, *S. emarginatum*, *P. costatus*, *T. atun*, *S. japonicus* and *Heteromycteris capensis*. The two species in this group whose larvae were not evident for the entire spawning period were *B. innornata* which were present in spring but absent in summer, and *Gaidropsarus capensis* which has a year-round spawning around the Cape Peninsula but was not encountered here in summer. Although the larvae of *L. hectoris* conformed to the known spawning periodicity of the species, with a winter peak,

they were encountered in shallower water than on the West Coast. The distance offshore of the shelf-break may have something to do with this, and if sampling had been undertaken as far as 90 km offshore from the study area the temporal patterns for this particular myctophid may have been different. Included amongst this group of conformers was the squid, *L. v. reynaudii* whose para-larvae provided evidence of spawning at times which had previously been recorded in the literature.

While conforming in part to published information on spawning seasonality, the presence of early life history stages of some species served as evidence for more prolonged spawning activity. Although larval densities of *E. japonicus* were at their maximum during the spring and summer period which is known to be their most active time, larvae were present in catches all year round. A similar situation existed with *S. sagax* whose concentrations conformed with previous winter peaks from the east coast, but they too were present all year round. The spawning season for *Genypterus capensis* is known to be protracted but all previous indications were that the earliest they started was March. A single larva caught near Bloukrans River in April showed that spawning was possible as early as February. Other species whose larval presence was indicative of a longer spawning season included *C. gymnoderma* (previously summer, now summer and autumn), *A. argyrozona* (season now includes winter months), and *C. laticeps* (larvae from August and March - a month earlier and a month later than previously recorded). There were also a couple of species which exhibited shifts in peak spawning activity when high larval concentrations were taken to mean maximum reproductive activity. The previous peak for *D. s. capensis* was spring/summer, but no larvae were encountered during the summer months and the peak was detected in winter. Similarly, summer has always been the peak breeding period for *T. t. capensis* and yet none of their larvae were caught at this time. Maximum catches were in winter and spring months. These instances are good examples of how the presence of eggs and larvae in the water can significantly add to the information on a species' spawning seasonality which may have been overlooked while sub-sampling from the adult population.

In the south-east Atlantic, larvae of *G. gonorhynchus* have historically been rare in catches, so the single specimen caught in this study is important to our further understanding of this species. The facts point to an August spawning on the south-east coast as opposed to what is known thus far for the west coast where larval presence points to February and June. Catches of *D. atlanticus* in the Benguela system on the other hand were good all year-round and yet their presence during

this work was rare. This was largely attributed to the mesopelagic existence of adults in deep water far offshore which would restrict the likelihood of their larvae being encountered too close inshore. The absence of any data from the east or west coast makes the *B. atlanticus* specimens that were caught a first, and they provide much needed information on spawning times. Although only a few of these larvae were caught, estimates for spawning times were in summer (late January to February) and winter (late June to July). All three goby species provided an excellent example of how similar strategies are employed within a group of fishes. Summer appeared to be either devoid of larvae or the least productive month, and autumn/winter emerged as the preferred seasons in which to spawn. This pattern is similar to that observed for the blenny species (except Species 5) where the upwelling season is avoided, a strategy also observed for species from the Benguela habitat. The converse appears true for *A. pectoralis* whose larvae had not yet been recorded from this region. Their apparent preference for spring and summer spawning means that larvae exist in the middle of the upwelling season. This behaviour appears to closely resemble that for the congeneric *A. microlepis* on the west coast where it is found most frequently in upwelling centres. Although larval *C. gymnoderma* have previously been sampled from the region (Tilney & Buxton 1994) there was no reference to it with respect to seasonality. Although only 33 were sampled during the three years of this study they were present in all four seasons with peaks in concentration during spring and autumn.

Aspects of the seasonality of certain larvae from the TNP were briefly discussed by Tilney & Buxton (1994). Individual species were not considered unless they were the only one within a family grouping, e.g. Engraulidae (*E. japonicus*) and Gadidae (*Gaidropsarus capensis*). Instead seasonal analysis was performed on the dominant families with spring/summer as one season and autumn/winter as another. With respect to *E. japonicus* and *G. capensis* similar patterns were observed by Tilney & Buxton (*op. cit.*) and during this study, with a spring/summer peak and a winter peak respectively. The absence of the latter species from summer catches in this study is the only discrepancy with the previous survey, although grouping spring and summer makes comparisons difficult. A peak in clupeid activity in winter and spring seems to be the pattern for this region as well, although both species (*S. sagax* and *E. whiteheadi*) are found in reasonable quantities all year. Gobiesocids were found in both the seasonal groupings by Tilney & Buxton (*op. cit.*) but were absent from summer in this study - again this could have been masked in the previous work by combining spring and summer. Members of the Cheilodactylidae were either only

recorded in winter (*C. fasciatus*) or were most dominant in winter during this study. Larvae from all three species were absent during summer. They appeared in both seasonal groups in Tilney & Buxton (*op. cit.*) but to a lesser extent in summer/spring where the true distribution could once again be masked. These authors also found an almost equal distribution of blenny larvae throughout the year. However, when individual species were examined in this study it was clear that most (including *P. pilicornis*) were winter/spring spawners, with only Blenniidae Species 5 showing a spring/summer peak in activity. The Cynoglossidae were present all year round in both studies, but Tilney & Buxton (*op. cit.*) declared *C. capensis* to be the dominant species, while *C. zanzibarensis* proved to be overwhelmingly dominant in this study. Both species were most abundant in winter and spring, with *C. capensis* being absent from summer samples, a pattern which is not clear from the grouped seasonal analysis performed in the previous survey which showed the summer/spring concentrations to be marginally higher. The only sole present in considerable quantities during this study was *A. pectoralis*, displaying a summer/spring peak. While the Soleidae also registered a springtime peak in the previous study (Tilney & Buxton *op. cit.*), their main species was *H. capensis*. Their other two soleid species, *S. bleekeri* and *Synaptura sp.*, either featured rarely or not at all in this study here, so comparison for seasonality is not feasible.

Adults and juveniles of many of the species represented in these catches are not resident but highly migratory or nomadic with a characteristically diffuse distribution, e.g. *T. atun*, *T.t. capensis*, *A. aequidens*, *S. japonicus*, *S. sagax*, *E. whiteheadi* and *E. japonicus*. These species may well fall into the category of those whose spawning grounds are not localised but are determined geographically depending on which prevailing conditions are favourable to larval survival (Sharp 1981; Iles & Sinclair 1982). Numerical swarmers such as *T.t. capensis*, *S. sagax* and *E. whiteheadi*, who take advantage of areas such as the study site and whose environmental conditions are relatively predictable from year to year, proved to be numerically dominant in catches for the duration of the study. The presence of *T. atun* in high concentrations on only one occasion (August 1993) on the other hand suggests that it may be a nomadic opportunist which demonstrates a degree of geographic flexibility, spawning wherever it is if conditions are right. Equally, it may reflect sampling error and a high degree of patchiness in distribution. If sea conditions in a geographic area change from their normal stable status quo one year, the reproductive success of the numerical swarmers who return there each season may be compromised because of poor larval survival. The nomadic opportunists who are more flexible would not be subject to such chronic

variability in survival (Sharp *op. cit.*) as they constantly roam the ocean in search of optimal feeding and spawning grounds, instead of needing to rely on a geographic area which proved optimal in the past. Another possible explanation for the lack of *T. atun* larvae in catches subsequent to August 1993, is that the spawner stock located offshore and to the east of the study area has been heavily fished since then, leading to a decline in population size and hence spawning efficiency.

The sporadic appearance of a few *A. aequidens* larvae in the catches is not enough to classify the spawning adults as nomadic opportunists, although it does pose some questions. Previous work has shown that adults do not spawn in the south-eastern Cape, but are instead highly migratory, moving up to KZN where they spawn in winter (Smale 1985; Griffiths 1988). Larvae have not been detected in the core of the Agulhas Current (Beckley 1993), and of the nine caught previously during east coast surveys, the majority have come from neritic waters between Durban and Port St. Johns. The remainder were found in samples taken over the 500 m isobath off Algoa Bay. The geelbek larvae from this study therefore provide a new record for the distributional extent of this species' early life history stages. It has been proposed that these larvae, together with those from other important linefish species, such as shad (*Pomatomus saltatrix*), *T. t. capensis*, several sparids (including *P. b. natalensis*), *P. olivaceum*, *S. japonicus*, and several serranids, utilise oceanographic features in the nearshore region for retention and dispersal southwards (Beckley *op. cit.*). It is unlikely that the few larvae caught in this study originated from KZN as their size and projected age would contradict the time it would have taken to reach this far south. On the other hand, their infrequent inclusion in collections mean that large spawning aggregations nearby are unlikely, and that perhaps only a few stray adults were responsible.

For many of the remaining species and for some already mentioned, numbers reflect the rarity with which they appeared in catches. Nevertheless their presence alone has some significance. In some cases, spawning seasons previously determined by traditional methods are confirmed or prolonged, e.g. *D. c. hottentotus*, *S. salpa*, *Genypterus capensis*, *C. fasciatus*, *L. richardsonii*, *M. cephalus*, *C. spinifer*, *S. kleini*, *Cynoglossus capensis*, *S. bleekeri* and *M. ocellatus*, and sometimes even exhibit marked differences, e.g. *Z. faber*. Other times they are among the first records of the larval stages in the region and provide vital information on the timing of spawning for species of which little or nothing is known about reproduction, e.g. *S. acus*, *L. caudatus*, *M. falciformis*, *Gymnammodytes capensis*, *A. capensis*, *S. emarginata* and Blenniidae Species 3 & 6.

Cheilodactylidae Species 1 & 2, Mugilidae Species 3, *C. spinifer*, *S. lalandi*, *D. atlanticus*, *G. gonorhynchus*, *B. atlanticus* and *Lophius upsicephalus*.

Spatial Distribution

The observed larval distribution patterns along the offshore transect were in agreement with the expected pattern based upon adult distribution and spawning habits for nine of the species present in any significant number. These included the pelagic-associated *S. sagax* and *L. hectoris*, the sand-associated *P. b. natalensis*, *T. t. capensis* and *C. zanzibarensis*, and the reef dwelling *C. gymnoderma*, *C. laticeps*, Cheilodactylidae Species 1 and *P. pilicornis*. A poor knowledge of the extent of the reef beyond the boundaries of the TNP makes it difficult to assume that larvae of species such as *C. laticeps* and Cheilodactylidae Species 1 originated from offshore where they were caught or inshore where an abundance of ideal reef habitat exists.

The larvae of another nine species were distributed differently to what was expected from an appraisal of adult behaviour and habitat. Larvae of *E. whiteheadi* were very patchy, with only eight specimens being recorded along the transect, none of which were out at 15 nm. Larvae of this species are susceptible to the gear, a total of 487 were caught during the entire study, so their absence must be explained by something else. Spawning may well have occurred outside of the sample area, but perhaps avoidance by larvae was largely responsible as catches were found to be higher at times of low light intensity during day/night catchability trials (see Chapter 3), and sampling over this 18 month period was only during daylight hours.

After encountering *E. japonicus* eggs on two occasions at inshore sites (see above) as well as larvae, it was anticipated that more of both eggs and larvae would be found in offshore samples. The once only larval presence at 15 nm, low concentrations at 10 nm, and no eggs at any sites was puzzling. The majority of larvae came from the five nm and Middlebank stations. It would appear as if spawning does occur further afield, with a considerable amount of larval drift inshore. It is possible that larvae are deep offshore and therefore not susceptible to capture in the upper 18.5 metres, but then migrate to shallower depths inshore. These supposed patterns of vertical distribution will be addressed in the next chapter.

Other species within this group of non-conformers were *Gaidropsarus capensis*, an inhabitant of tide pools and subtidal reefs down to 50 metres, whose larvae were sampled as

far offshore as 10 nm. *Chelidonichthys capensis* is found at extreme depths far offshore and yet its larvae were absent from the 15 nm stations while being present frequently at the other sites. Likewise the lack of *P. olivaceum* larvae at 15 nm and in spring/summer months is unusual as the adults are supposed to be deepwater spawners at these times (Smith & McKay 1986). Adult *A. argyrozona* can be found inshore and to depths of 200 metres, but this survey did not reveal any larvae at 15 nm and they were found only once out at 10 nm. *Diplodus sargus capensis* is a common intertidal and subtidal (to 25 metres) resident, whose larvae must be prone to offshore drift, as specimens were found at the distant five and ten nm stations. Adults of both *P. costatus* and *A. pectoralis* are found offshore to considerable depths, yet in each case no larvae were ever sampled at the furthest site 15 nm offshore.

In this chapter, the temporal and spatial (horizontal/offshore) distributional patterns of fish and squid larvae from the study area have been ascertained. The lack of any differentiation in abundance between sites along the offshore transect leads to the preliminary conclusion that up to 15 nm offshore from Storms River mouth, there is one continuous larval species assemblage. This could be a similar case to that described by McGowen (1993) for alongshore assemblage patterns which are either difficult to detect or comprise changes in relative abundance rather than species composition. The chances of detecting different assemblages increase when biotic or abiotic boundaries are present which may be responsible for separation of two groups. The samples from the transect were all taken in the surface (0 - 18.5 metres) layers only. In the next chapter samples are taken from the entire water column where physical barriers such as thermoclines and pycnoclines may reveal more about the larval species assemblages along the south-east Cape coast.

CHAPTER 6 - A PRELIMINARY INVESTIGATION INTO THE VERTICAL DISTRIBUTION OF EGGS AND LARVAE IN RELATION TO HYDROGRAPHICAL FEATURES

INTRODUCTION

While a host of factors may be responsible for the occurrence, abundance and observed distributional patterns of ichthyoplankton (Doyle, Morse & Kendall 1993), Bakun (1988 in Boehlert, Watson & Sun 1992) stresses that information specifically about vertical distribution and the physical environment (oceanography) are required in order to fully understand them. According to Smith & Stoner (1993) computer simulations showed that the vertical distribution of planktonic larvae is a product of vertical migration and turbulent diffusion which act to concentrate larvae or produce vertically uniform concentrations respectively. Distributional patterns of eggs and early larvae coupled with oceanographic information contribute to the greater understanding of recruitment through specific spawning requirements and conditions for early stage survival (Cushing 1967; Norcross, Richardson, Massmann & Joseph 1974; Williams & Hart 1974; Alshuth 1989; Palomera & Sabatés 1989), e.g. spawning in the cod *Gadus morhua*, and the bristlemouth *Maurolicus muelleri* may be linked to primary and secondary production in the Irish and North Sea, and North East Atlantic respectively (Williams & Hart *op. cit.*; Brander 1989). In comparison to the horizontal dimension, physical and biotic parameters exhibit severe stratification into narrow depth zones in the vertical dimension (Kauffman, Lindsay & Leithiser 1981; Saville & Schnack 1981; Brodeur & Rugen 1994). As such, studies attempting to discern survival and recruitment patterns must first determine the exact vertical distribution of larvae. Patterns of larval abundance and distribution are influenced both directly and indirectly on temporal scales ranging from evolutionary to diurnal, and spatial scales from 1000 to < 100 km^2 (Doyle *et al. op. cit.*). According to these authors the distributional range of adult populations and their spawning strategies operate on a larger spatial and longer temporal scale and are the starting point for all ichthyoplankton distribution. Mesoscale variation over smaller areas and over time periods down to 24 hours result from physical and biological factors acting directly on larvae.

Ultimately, the factors fisheries biologists should be using to explain observed patterns are water temperature (e.g. thermoclines) and chemistry, larval drift, bioenergetic optimisation, food availability and digestion cycles, predator abundance and avoidance, light intensity, larval growth,

development and survival, and larval behaviour (Kendall & Naplin 1981; Kerfoot 1985; Wartsbaugh & Neverman 1988; Lampert 1989; Kendall, Incze, Ortner, Cummings & Brown 1994; Gray 1993, 1996; Olivar & Sabatés 1997). Larval behaviour incorporates vertical migration or placement to take advantage of optimal conditions for feeding, predator avoidance, thermoregulation and osmoregulation, retention, and directed transport/dispersal by currents (Norcross & Shaw 1984; Sinclair 1988; North & Ward 1989; Lenarz, Larson & Ralston 1991; North & Murray 1992; Lough & Potter 1993). For example, the sculpin *Gilbertidia sigalutes* limits the extent to which surface currents disperse the early stages by regular crepuscular and nocturnal migrations into sub-surface layers which are characterised by slower countercurrents (Marliave 1981), and *Sardina pilchardus* appears to spawn nocturnally in waters off Portugal to avoid diurnally active planktivores (Ré, Farinha & Meneses 1989). Discrete depth sampling accompanied by oceanographic and water chemistry data can reveal much about the preferences of larvae for certain of these conditions, both physical (currents, temperature tolerance and chemistry) and biological (feeding and predation). Additional information which can be gained from vertical distribution studies include the duration of the pelagic phase, the speed and sequence of fin, notochord and muscular development, and buoyancy control of eggs and larvae.

A knowledge of the vertical stratification of a species' early stages can also significantly decrease effort during future surveys and prevent waste of limited ship time. In an earlier study, Sameoto (1982) showed that Peruvian anchovy (*E. ringens*) larvae were restricted to the upper 50 metres off the coast of Peru, which meant that future works needed only to sample in this strata instead of over the entire water column. In practical terms, knowledge of the depth distribution characteristics of a species can ensure adequate sampling of the correct depth range if accurate abundance estimates are to be made (Kendall & Naplin 1981; Brodeur & Rugen 1994), i.e. sampling only surface layers can lead to drastic underestimates if the species concerned has an extensive vertical range. For example, while most larvae of the species assemblage found in Cumberland East Bay, South Georgia, were found shallower than 150 m (North & Murray 1992), peak densities of the myctophid *Electrona antarctica* were between 150 to 200 m during the day and even deeper at night in spring months.

There is a paucity of works on the vertical distribution of larval fish in southern African waters. Of the few that have been done, most have been restricted to the west coast (Olivar & Rubiés

1983, 1987; Olivar 1990; Olivar & Fortuño 1991), with only a brief description of some dominant taxa along the east coast (Beckley 1994). Also lacking is a knowledge of the relationship between larval distribution and physical and biological factors. The gathering of these data is essential to our understanding of the dynamics of fish eggs and larvae in the nearshore zone. A more complete understanding of what determines ichthyoplankton patchiness can only lead to more efficient sampling programs as well as enable specific questions to be answered. The equipment required for combined studies such as this is expensive, and yet it is available onboard the R.S. *Africana* and R.S. *Algoa*. Dedicated ship time is required but seldom obtained for these studies, and until this happens, nearshore ichthyoplankton research in South Africa can only stumble forward when it should be going ahead in leaps and bounds.

A single larval species assemblage was detected from the offshore transect work described in Chapter 5. In order to determine whether this single assemblage extended in three dimensions, a preliminary appraisal of the vertical distribution of ichthyoplankton in the study site was undertaken. It was anticipated that discrete depth sampling would reveal the presence of another discrete species assemblage in deeper waters, in addition to the short term vertical migratory patterns. Due to limited ship time and the anticipated small data set, this aspect of the study was only considered as being pre-emptive to later, more detailed surveys.

Spatial variability characterises the distribution of most planktonic animals (Cowen, Hare & Fahay 1993) including fish larvae. Fisheries scientists have long been looking for answers as to the causal effects, both physical processes and biological adaptations, which influence larval retention or transport, behind this phenomenon. Where possible, observations are coupled with data on physical (currents and nutrients) and biological (zooplankton volume) aspects. The vertical distribution of ichthyoplankton and how it affects the interpretation of data obtained from bongos from only a section of the water column is also discussed.

MATERIALS AND METHODS

Discrete depth sampling was performed on two occasions while on board the R.S. *Africana*, during voyage #131 (September/October 1995) and voyage #135 (April 1996). Sample times and sites were described in detail in Chapter 1. The depths which were sampled depended on the vertical temperature profile which was obtained from real time data as the RMT1x6 net was lowered through the water column. The net was lowered at a speed of 1 m/s^{1} and retrieved at 0.5

m/s^1, and filtered volume was electronically recorded with a General Oceanics digital flow meter mounted on the frame of the net. Samples were handled following the protocol outlined in Chapter 2.

The larval concentrations and mean sizes for inshore samples from voyage #131 were analysed by a Kruskal-Wallis ANOVA by ranks test, while a 2-way ANOVA was used to test the combined data from the two days. Larval concentrations from offshore stations were analysed by a 2-way ANOVA for each day and a 3-way ANOVA for combined days. Similarly, a 2-way and 3-way ANOVA were applied to the mean larval size data from each day and combined days respectively.

The same analysis used for voyage #131 offshore samples was applied to the concentration and size data from voyage #135. When data from both days were combined, however, the midday values from day 1 were excluded. When statistical differences were detected in any of the ANOVA's conducted, Tukey's multiple-range test was applied to determine the source.

Four regression models, namely linear ($Y = a + bX$), multiplicative ($Y = a*X^{b}$), exponential ($Y = \exp[a + bX]$), and reciprocal ($1/Y = a + bX$), where a is the intercept and b the slope, were applied to the ichthyoplankton, plankton and CTD data. The designation of a* in some of the multiplicative models indicates that the intercept is equal to Log a. All four models were applied to the data using the STATGRAPHICS package, and the one providing the best fit (highest R^2 value) was used.

RESULTS

Voyage #131 inshore

Because the well mixed water column inshore the depth strata sampled were chosen so as to include the top 10 meters and the bottom half of the profile, with the middel layer including the stratum in between. The three depth strata sampled were the surface layer (0 - 10.4 m), middle layer (10.4 - 17.5 m), and deep layer (> 17.5 m). A total of 196.16 m^3 of water was filtered from the inshore sites at an average of 49.04 ± 10 m^3 per tow. Days 1 and 2 produced a total of 87 larvae (62 & 25 respectively) comprising 19 species from 12 families (Table 6.1). Of these, 14 species from nine families were not present frequently enough or in sufficient numbers for further analysis. Anchovy eggs totalled 2 998, while all other eggs totalled 122. Squid para-larva concentrations were low (Table 6.1) with a total of three being caught on the first day and four on the second.

Table 6.1 - Concentrations of fish eggs and larvae and squid para-larvae caught at three depth intervals inshore at Elands River on the 7th & 8th October 1995 during voyage #131 aboard the R.S. *Africana* (* species precluded from further analysis).

FAMILY	SPECIES	DEPTH	CONCENTRATION	
			DAY 1	DAY 2
Clupeidae	*E. whiteheadi*	>17.5	0.034	0.034
		17.5-10.4		
		10.4-0		0.115
	S. sagax	>17.5	0.308	
		17.5-10.4	0.276	0.04
		10.4-0		
Tetrarogidae	*C. gymnoderma**	>17.5		
		17.5-10.4		0.04
		10.4-0		
Gadidae	*G. capensis**	>17.5		
		17.5-10.4		
		10.4-0		0.023
Cynoglossidae	*C. zanzibarensis*	>17.5	0.274	0.026
		17.5-10.4	0.039	
		10.4-0		
Soleidae	*H. capensis**	>17.5	0.034	
		17.5-10.4		
		10.4-0		
	*A. pectoralis**	>17.5		
		17.5-10.4		0.04
		10.4-0		
	S. kleini*	>17.5	0.034	
		17.5-10.4		
		10.4-0		
Callionymidae	*P. costatus*	>17.5	0.103	0.053
		17.5-10.4	0.551	
		10.4-0		
Gobiesocidae	Species 1*	>17.5		0.053
		17.5-10.4	0.039	
		10.4-0		
	Species 2*	>17.5		
		17.5-10.4		0.079
		10.4-0		
Bregmacerotidae	*B. atlanticus**	>17.5		0.026
		17.5-10.4		
		10.4-0		
Sparidae	Species 6*	>17.5		
		17.5-10.4		
		10.4-0	0.029	
Gobiidae	Species 1	>17.5	0.034	0.079
		17.5-10.4	0.039	0.04
		10.4-0		
	Species 2*	>17.5	0.103	
		17.5-10.4		
		10.4-0		
Engraulidae	*E. japonicus**	>17.5		0.053
		17.5-10.4	0.039	
		10.4-0		
Blenniidae	*P. pilicornis*	>17.5		
		17.5-10.4		0.04
		10.4-0		
	Species 3*	>17.5		
		17.5-10.4		
		10.4-0	0.115	
	Species 5*	>17.5		
		17.5-10.4	0.039	
		10.4-0	0.058	

Table 6.1 continued

FAMILY	SPECIES	DEPTH	CONCENTRATION	
			DAY 1	DAY 2
Total Larvae		>17.5	0.958	0.315
		17.5-10.4	1.063	0.277
		10.4-0	0.201	0.138
E. japonicus Eggs		>17.5	23.871	0.552
		17.5-10.4	65.683	0.911
		10.4-0	12.845	3.224
Other Eggs		>17.5	0.171	0.473
		17.5-10.4	0.512	0.911
		10.4-0	0.805	0.806
Loliginidae	*L. v. reynaudii*	>17.5	0.034	
		17.5-10.4	0.079	
		10.4-0		0.092

The temperature profile for inshore stations on both days showed a well mixed, stable water column with values ranging from 17.5°C at the surface to 17.0°C just above the bottom at 33 metres. Data logged from the CTD rosette sampler on the second day are presented in Table 6.2. With the exception of salinity, which was stable throughout the water column, all other physical parameters showed very little variation. Oxygen, silicate and chlorophyll levels generally decreased with depth, while those of nitrate, nitrite and phosphate increased.

The general trend for individual species of fish larvae over the two days was for maximum concentrations to be found in the deep or middle layer. The single exception to this was *E. whiteheadi* on day 2, which displayed a highest concentration in the surface layer (Table 6.1). A trend of maximum concentration in the middle layer was observed for all fish eggs, total larvae, and squid larvae on day 1, but only for round eggs on day 2, when *E. japonicus* eggs, squid larvae and total larvae were mostly concentrated at the surface (Table 6.1). There were, however, no significant differences at the 95% level between concentrations of any larvae, eggs or squid in all three layers. Looking at both days combined, there were significantly higher concentrations of *C. zanzibarensis* in the deep layer compared to the surface ($F_{5.902}$; $P < 0.05$). For the rest, concentrations were not significantly different between layers or days, nor was there any interaction detected between depth and day.

The occurrence of most species at a single depth, or at multiple depths but from only one day, meant that only a few could be subjected to mean size comparisons. The mean size of *S. sagax*, *P.*

costatus, Gobiidae Species 1 and *L. v. reynaudii* larvae on day 1 was larger in the deepest layer compared to the mid-layer, although the difference was not significant. On day 2 only *E. whiteheadi* and Gobiidae Species 1 were present in more than one layer (Table 6.1), with the mean size of the former species being larger, but not significantly so, in the deepest strata compared to the surface. The mean size of the goby species in the lower two layers was equal. The 2-way ANOVA performed on size data from both days combined revealed that the only significant differences were between days and not between depth levels.

Voyage #131 offshore

The water column was divided into the following strata, surface (0 - 10.6 m), middle (10.6 - 45 m), and deep (> 45 m). The middle layer incorporated the thermocline which was usually present between 30 and 45 metres. A total of 1 340.05 m^3 of water was filtered from 12 tows at the offshore sites, with an average filtered volume per tow of 111.67 ± 35.04 m^3. The offshore environment produced 834 larvae comprising 29 species from 20 families (Table 6.3). Due to their infrequent appearance in samples and overall low concentrations, 19 of these species representing 14 families could not be included in further analysis. Seven hundred *Engraulis japonicus* eggs were caught on the first day with almost twice as many (1 367) on the second day, while similar numbers of other eggs (1039 & 1383) were caught on days 1 and 2 respectively. A single squid para-larva was caught on the first day, with four being sampled the following day.

Physical parameters

The temperature profiles recorded during the 21h00 and 23h00 samples on day 1 were similar, with temperatures ranging between 17.6°C at the surface and 9.9°C at 84 metres. The thermocline was situated between 36 and 59 metres where the temperature had dropped to 11.3°C. By 01h00 surface and bottom temperatures were between 18.3°C and 11.0°C, with the thermocline having moved shallower to between 31 and 51 metres.

On day 2, surface and bottom temperatures ranged from 17.4 to 18.2°C and 12.2 to 10.0°C respectively. The thermocline, situated between 31 and 66 metres at 21h00 moved shallower to 56 metres at 23h00 and showed signs of breaking up by 21h00, when a gradual decrease in temperature instead of a sudden decline was evident.

Table 6.2 - CTD data for Elands River RMT1x6 stations, inshore on the 8th October and offshore on the 7th & 8th October 1995, at different time intervals.

INSHORE	DEPTH (M)			
DAY 2 - 19h00	0	10	21	39
Salinity - o/oo	35.38	35.38	35.38	35.38
Oxygen - umol.l^{-1}	5.92	5.78	5.72	5.41
Nitrate - umol.l^{-1}	0.62	0.78	0.66	1.18
Nitrite - umol.l^{-1}	0.03	0.118	0.05	0.12
Silicate - umol.l^{-1}	3.68	2	2.1	3
Phosphate - umol.l^{-1}	0.3	0.32	0.36	0.43
Chlorophyll a - umol.l^{-1}	1.1	0.95	1.1	0.68

OFFSHORE	DEPTH (M)					
DAY 1 - 23h00	0	10	21	40	61	76
Salinity - o/oo	35.41	35.41	35.41	35.41	34.91	34.89
Oxygen - umol.l^{-1}	5.7	5.62	5.58	5.2	4	3.93
Nitrate - umol.l^{-1}	0.7	0.6	0	1.6	19.27	20
Nitrite - umol.l^{-1}	0.15	0.04	0.03	0.26	0.13	0.1
Silicate - umol.l^{-1}	2.7	3	2.63	2.98	15.1	15
Phosphate - umol.l^{-1}	0.3	0.34	0.3	0.33	1.58	1.62
Chlorophyll a - umol.l^{-1}	0.87	0.87	1.12	0.5	0.14	

OFFSHORE (DAY 2)	TIME	DEPTH (M) AT EACH TIME					
	21h20	0	12	22	32	51	62
	22h55	0	11	21	31	52	80
	00h51	0	9	20	36	51	76
Salinity - o/oo	**21h20**	35.43	35.43	35.43	34.34	35.25	35.27
	22h55	35.41	35.41	35.41	35.39	35.28	34.89
	00h51	35.43	35.43	35.43	35.43	35.3	35.25
Oxygen - umol.l^{-1}	**21h20**	5.6	5.57	5.74	5.2	4.55	4.51
	22h55	5.7	5.7	6	5.7	4.3	4.3
	00h51	5.3	5.3	5.3	5.15	4.5	4.62
Nitrate - umol.l^{-1}	**21h20**	2.53	2.53	1.1	2.81	8.4	13.11
	22h55	2.35	2.35	1.1	1.1	10.1	16.8
	00h51	1.85	1.12	1.12	1.85	10.8	12.03
Nitrite - umol.l^{-1}	**21h20**	0.14	0.12	0.12	0.3	0.32	0.19
	22h55	0.15	0.18	0.12	0.15	0.19	0.29
	00h51	0.11	0.06	0.06	0.11	0.14	0.11
Silicate - umol.l^{-1}	**21h20**	4.02	3.98	3.2	3.81	7.6	7.69
	22h55	3.79	3.79	2.5	2.1	6.2	10.53
	00h51	4.8	3.21	3.21	3.21	6.2	5.88
Phosphate - umol.l^{-1}	**21h20**	0.63	0.48	0.45	0.54	0.84	1.15
	22h55	0.58	0.39	0.58	0.39	0.95	1.48
	00h51	0.47	0.45	0.41	0.41	0.78	1.08
Chlorophyll a - umol.l^{-1}	**21h20**	0.35	0.35	1.01	0.35	0.37	-
	22h55	0.47	0.47	1.55	0.78	0.23	-
	00h51	0.91	0.89	1.1	0.89	0.001	-

CTD data for both days are presented in Table 6.2. In all instances, salinity displayed a high degree of stability throughout the water column, while oxygen levels remained relatively stable above the thermocline before decreasing in the deeper layer. Nitrite levels tended to decrease slightly into the middle layer after which they displayed considerable variation within and below the thermocline. Nitrate, silicate and phosphate levels all registered low values between the surface and approximately 40 metres, after which marked increases were recorded through and below the thermocline. Chlorophyll-a values followed the same trend as was observed for oxygen, with the lowest levels being recorded in the deepest stations.

Larval distribution

Larvae of *E. whiteheadi* were restricted to the middle and deep layers on both days (Table 6.3), and while concentrations caught at each time over the period did not differ significantly, the overall abundance of larvae in the middle layer on day 2 was found to be significantly higher than in the deep ($F_{.}$ 4.854; $P < 0.05$). This result, however, has been based on a small data set and should be regarded as tentative. The same applies to all quoted statistical results which follow in this section. Mean size of larvae caught on both days exhibited no significant differences.

Catches of *S. sagax* on day 1 represented an even distribution throughout the water column, with perhaps a slight preference for the middle stratum (Table 6.3). Statistically, however, no preference for a specific depth was indicated and a homogeneous distribution over time was confirmed. On day 2, most larvae were present in samples from the top two layers, being recorded in the deep layer only once (Table 6.3). The preference was clearly for the middle reaches at all times, with the concentrations there being significantly higher than elsewhere ($F_{.}$ 23.347; $P < 0.05$). A possible explanation is that larvae were more prone to capture in the cooler thermocline waters, and as visibility decreased through the night. Mean sizes of larvae on day 1 were evenly distributed with respect to depth. On the second day, larvae in the deep water were similar in size to those from the surface but significantly greater than those from the middle layer ($F_{.}$ 3.236; $P < 0.05$).

A definite preference for the middle and deep layer was exhibited by *P. costatus* (Table 6.3). Although distribution over depth and time was not significantly different, indications were that the middle layer was preferred during the later stages of night. This was more evident from day 2 catches where initially high catches in the deep layer were reduced in later samples while catches in

Table 6.3 - Concentrations of fish eggs and larvae and squid para-larvae caught at three depth intervals offshore at Elands River on the 7th & 8th October 1995 during voyage #131 aboard the R.S. *Africana* (* species precluded from further analysis).

FAMILY	SPECIES	DEPTH	CONCENTRATION - DAY 1			CONCENTRATION - DAY 2		
			21H00	23H00	01H00	21H00	23H00	01H00
Clupeidae	*E. whiteheadi*	>45.0	0.051	0.042			0.015	
		45-10.6		0.02	0.078	0.041	0.082	0.121
		10.6-0						
	S. sagax	>45.0	0.038	0.008				0.006
		45-10.6	0.096	0.12	0.389	0.172	0.106	0.64
		10.6-0	0.064	0.086	0.018	0.016	0.025	0.11
Gadidae	*G. capensis**	>45.0						
		45-10.6	0.009					
		10.6-0						
Callionymidae	*P. costatus*	>45.0	0.203	0.051		0.749	0.031	0.006
		45-10.6	0.287	0.301	0.078	0.59	0.522	0.43
		10.6-0						
Cynoglossidae	*C. capensis**	>45.0	0.013	0.008				
		45-10.6						
		10.6-0						
	C. zanzibarensis	>45.0	0.013	0.042		0.091		
		45-10.6	0.087	0.04	0.026	0.123	0.065	0.038
		10.6-0						
Soleidae	*H. capensis**	>45.0						
		45-10.6	0.009					
		10.6-0						
	*A. pectoralis**	>45.0		0.008				
		45-10.6						
		10.6-0						
Gobiesocidae	Species 1*	>45.0		0.008				
		45-10.6						
		10.6-0						
	Species 2*	>45.0		0.008				
		45-10.6						
		10.6-0						
Sparidae	*B. inornata**	>45.0						
		45-10.6					0.041	0.151
		10.6-0						
	Species 6*	>45.0						
		45-10.6						0.015
		10.6-0						
Carangidae	*T. trachurus*	>45.0		0.025				
		45-10.6			0.078		0.016	0.544
		10.6-0						0.074
Gobiidae	Species 1	>45.0	0.013	0.05		0.073		
		45-10.6	0.009			0.025		0.008
		10.6-0						
	Species 2	>45.0	0.013	0.076				0.018
		45-10.6			0.13		0.016	0.136
		10.6-0	0.192	0.043				
	Species 3*	>45.0		0.017		0.018		
		45-10.6						
		10.6-0						

Table 6.3 continued.

FAMILY	SPECIES	DEPTH	CONCENTRATION - DAY 1			CONCENTRATION - DAY 2		
			21H00	23H00	01H00	21H00	23H00	01H00
Merlucciidae	*M. capensis*	>45.0					0.077	
		45-10.6				0.041	0.041	
		10.6-0						0.037
Engraulidae	*E. japonicus**	>45.0						
		45-10.6			0.026		0.008	
		10.6-0						
Triglidae	*C. capensis*	>45.0						
		45-10.6	0.035	0.02			0.008	0.023
		10.6-0						
Scombridae	*S. japonicus*	>45.0		0.042				
		45-10.6		0.006			0.073	
		10.6-0						
Lophiidae	*L. vomerinus**	>45.0						
		45-10.6				0.008		
		10.6-0						
Congiopodidae	*C. spinifer**	>45.0						
		45-10.6					0.008	
		10.6-0						
Moridae	*P. capensis**	>45.0						0.012
		45-10.6					0.008	
		10.6-0						
Myctophidae	*D. atlanticus**	>45.0						0.006
		45-10.6						
		10.6-0						
	*S. barnardi**	>45.0						0.012
		45-10.6						0.015
		10.6-0						
	*L. hectoris**	>45.0						
		45-10.6						0.015
		10.6-0						
Ophidiidae	*G. capensis**	>45.0						0.006
		45-10.6						
		10.6-0						
Trichiuridae	*L. caudatus**	>45.0						
		45-10.6						0.06
		10.6-0						
Sciaenidae	Species 1*	>45.0						
		45-10.6						0.008
		10.6-0						
Total Larvae		>45.0	0.38	0.387		0.931	0.124	0.074
		45-10.6	0.539	0.661	1.012	0.999	0.995	2.205
		10.6-0	0.255	0.216	0.017	0.016	0.025	0.221
E. japonicus Eggs		>45.0	1.889	3.349		0.037	0.077	
		45-10.6	1.027	0.241		1.622	5.503	0.045
		10.6-0	1.277	0.129		2.641	7.626	
Other Eggs		>45.0	2.346	3.492	0.523	0.347	0.788	0.567
		45-10.6	0.818	1.824	2.283	1.106	3.864	1.609
		10.6-0	2.171	4.01		0.28	4.29	7.571
Loliginidae	*L. v. reynaudii*	>45.0						0.006
		45-10.6					0.008	0.015
		10.6-0	0.064					

the middle layer reflected a significant increase during later stages and a preference by larvae for that depth (F. 6.224; $P < 0.05$). No difference in sizes of larvae at depth could be found for day 1 samples, but differences were detected on the second day, with larvae from the deep water being larger than in the middle layer (F. 7.472; $P < 0.05$). This same trend was observed for combined data from both days with the largest mean sizes being recorded in the deep water (F. 4.525; $P < 0.05$).

The vertical distribution of *Cynoglossus zanzibarensis* was similar to that of *P. costatus*, with the majority being found in the middle layer and none at the surface (Table 6.3). Whether larvae are migrating into the mid-stratum as the night progresses is difficult to discern. Catches on day 1 were found to be evenly distributed, but a preference for the middle layer was found on day 2 (F. 26.707; $P < 0.05$). There was no significant difference in the mean size of larvae from the two depths over both days.

Trachurus t. capensis larvae were patchily distributed throughout the water column over the two days (Table 6.3). Looking at concentrations, it appeared as if the middle layer was preferred, but this was not supported statistically. A statistical difference in mean size was detected between the deep and middle layers on day 1 (F. 14.45; $P < 0.05$) with larger specimens in the deeper water.

Concentrations of Gobiidae Species 1 were low (Table 6.3) which meant that little could be determined from statistical analysis. Gobiidae Species 2 was present more frequently and mostly in higher concentrations. However, the limited data base once again prevented any meaningful statistical analysis.

There were no *Merluccius capensis* larvae in catches from the first day, but they were present at all three sample times and in all depths on day 2 (Table 6.3). This result highlights the problems of both patchinesss and a limited sampling regime which fails to determine larval preferences with respect to depth. While the mean size of *M. capensis* larvae was greater in the surface layer, followed by those in the middle and lastly the deep, the differences were not significant.

Concentrations of *Chelidonichthys capensis* larvae were on the low side, but all were found in the middle layer on both days (Table 6.3). Larvae of *C. capensis* were absent from the 01h00

sample on day 1 and the 21h00 sample on the second day, but their absence from other layers at these times as well points to movement away from the sample area or avoidance rather than a vertical movement out of the layer. Although a significant difference was detected between depth ($F_{2,15.369}$; $P < 0.05$), the poor representation in catches and small data base means this must be treated carefully. There were no detectable differences in mean size of larvae from different depths.

The distribution of *E. japonicus* eggs on day 1 showed maximum concentrations in the deep waters (Table 6.3), but this was not found to be significant. On the second day, however, the situation was vastly different, with only a few being found in the deep layer (Table 6.3). These patterns of distribution were found to be significantly different, with concentrations at the surface being higher than those in the middle which were in turn significantly higher than in the deep ($F_{2,17.232}$; $P < 0.05$). The virtual absence of *E. japonicus* eggs from the 01h00 stations on both days, and the low concentrations in the deep layer on day 2 once again indicate extreme patchiness and highlight the need for more extensive surveys.

Despite the absence of other eggs in the surface layer at 01h00 on day 1 (Table 6.3), their overall distribution was found to be homogeneous with respect to depth. As for the eggs of *E. japonicus*, differences in distribution were evident on the second day. Eggs were present at all times and at all depths, with significantly greater concentrations being found at the surface compared to the middle and deep layer. Concentrations between the two deeper layers also differed significantly ($F_{2,17.038}$; $P < 0.05$).

Voyage #135

During this voyage the three depth strata which were sampled off Bloukrans River were the surface (0-10.6 m), middle (10.6-30.5 m) and deep (> 30.5 m) layer. A total of 2 179.2 m^3 of water was sampled over the two days at an average of 155.66 ± 23.49 m^3 per tow. Egg quantities were considerably lower than those from voyage #131, with no *E. japonicus* eggs and only 489 others being caught. The number of larvae was also considerably less with only 252 being caught. Twenty-three species of larvae from 17 families were identified from the samples. Of these, 15 species from 13 families (Table 6.4) were not considered for further analysis because of poor representation. Seven squid para-larvae were caught.

Table 6.4 - Concentrations of fish eggs and larvae and squid para-larvae caught at three depth intervals at Bloukrans River on the 25th & 26th April 1996 during voyage #135 aboard the R.S. *Africana* (* species precluded from further analysis).

FAMILY	SPECIES	DEPTH	CONCENTRATION - DAY 1				CONCENTRATION - DAY 2		
			S/R	M/D	S/S	M/N	S/R	S/S	M/N
Clupeidae	*E. whiteheadi*	**>30.5**	0.051	0.006	0.034	0.154	0.02		0.024
		30.5-10.6	0.008		0.036	0.163			
		10.6-0	0.011	0.025	0.07	0.077	0.031		
Sparidae	Species 10*	**>30.5**	0.006						
		30.5-10.6							
		10.6-0							
Cynoglossidae	*C. capensis**	**>30.5**			0.007				
		30.5-10.6	0.008						
		10.6-0							
	C. zanzibarensis	**>30.5**			0.007	0.019		0.015	
		30.5-10.6	0.008		0.018	0.018			
		10.6-0	0.011	0.025	0.042	0.077		0.095	0.019
Callionymidae	*P. costatus*	**>30.5**	0.006	0.012	0.021	0.019		0.037	0.035
		30.5-10.6		0.01	0.009	0.036			
		10.6-0		0.025					
Triglidae	*C. capensis**	**>30.5**		0.006					
		30.5-10.6							
		10.6-0							
Cheilodactylidae	Species 1	**>30.5**							
		30.5-10.6					0.019		
		10.6-0		0.013					
Soleidae	*A. pectoralis*	**>30.5**			0.007	0.019			
		30.5-10.6		0.039	0.009		0.028		
		10.6-0	0.023	0.013	0.026		0.031		0.019
	*H. capensis**	**>30.5**							
		30.5-10.6						0.007	
		10.6-0		0.013					
	*M. ocellatus**	**>30.5**							
		30.5-10.6						0.014	
		10.6-0				0.039			
Merlucciidae	*M. capensis*	**>30.5**	0.013	0.024	0.021	0.025		0.029	0.021
		30.5-10.6	0.016	0.02			0.009		
		10.6-0	0.011	0.013				0.012	
Gobiidae	Species 1	**>30.5**		0.006	0.014	0.006			
		30.5-10.6	0.008	0.01	0.018	0.036		0.014	
		10.6-0			0.042			0.012	0.019
	Species 2	**>30.5**		0.006		0.006	0.007	0.007	
		30.5-10.6	0.039	0.01			0.009		0.023
		10.6-0						0.048	
	Species 3	**>30.5**	0.038	0.006	0.007	0.006			0.014
		30.5-10.6		0.01	0.009	0.018			
		10.6-0				0.077			
Syngnathidae	*S. acus**	**>30.5**							
		30.5-10.6							
		10.6-0		0.013					
Ophidiidae	*G. capensis**	**>30.5**				0.006			
		30.5-10.6							
		10.6-0							

Table 6.4 continued

FAMILY	SPECIES	DEPTH	CONCENTRATION - DAY 1				CONCENTRATION - DAY 2		
			S/R	M/D	S/S	M/N	S/R	S/S	M/N
Gobiesocidae	Species 2*	>30.5				0.006			
		30.5-10.6						0.014	
		10.6-0							
	Species 3*	>30.5						0.007	
		30.5-10.6							0.023
		10.6-0							
Ammodytidae	*G. capensis**	>30.5				0.006			
		30.5-10.6							
		10.6-0							
Carangidae	*S. lalandi**	>30.5					0.007		
		30.5-10.6							
		10.6-0							
Congiopodidae	*C. spinifer**	>30.5					0.007		
		30.5-10.6							
		10.6-0							
Bregmacerotidae	*B. atlanticus**	>30.5							
		30.5-10.6							
		10.6-0							0.019
Engraulidae	*E. japonicus**	>30.5				0.006			
		30.5-10.6							
		10.6-0			0.028			0.024	
Total Larvae		>30.5	0.115	0.066	0.117	0.283	0.039	0.102	0.069
		30.5-10.6	0.093	0.07	0.1	0.271	0.085	0.041	0.034
		10.6-0	0.056	0.139	0.24	0.288	0.062	0.214	0.076
Egg Totals		>30.5	0.5	0.125	0.014	0.411	0.026	0.095	0.014
		30.5-10.6	0.062	0.03	0.009	0.09	0.16	0.083	0.239
		10.6-0	0.237	0.56	0.608	0.154	0.59	1.069	0.359
Loliginidae	*L. v. reynaudii*	>30.5	0.006		0.014	0.006			0.007
		30.5-10.6		0.01				0.014	
		10.6-0							

Physical parameters

The depth/temperature profile on day 1 was characterised by a shallow thermocline which ranged from between 7 and 17 metres at sunrise, 2 and 17 metres at midday and midnight, and from the surface down to 16 metres at sunset. Surface temperatures were cool, ranging from 14.9 to 17.5°C, with lows of between 9.8 and 10.2°C being recorded at the bottom of the thermocline.

Sunrise on day 2 saw evidence that the thermocline had breached the surface, with the surface temperature measuring 12.3°C. The bottom of the cold wedge had also moved shallower as temperatures levelled out at 10.2°C at 10 metres and remained relatively stable to 57 metres. Although the thermocline had slipped below the surface and extended to 15 metres at sunset, by

midnight it had again broken through the surface layer and moved shallower. Temperatures were similar to those observed at sunrise.

CTD data for both days are presented in Table 6.5. For the most part, trends and values were similar to those observed during the previous voyage (#131), with oxygen and chlorophyll-a values decreasing with depth, while levels of nitrate, nitrite, silicate and phosphate all displayed steady increases through the thermocline, registering maximum values in the deeper layers. Both nitrate and chlorophyll-a values in the surface layers were markedly higher than those observed during voyage #131, perhaps due to the proximity of the thermocline to the surface resulting in high levels of primary production and plankton blooms.

Table 6.5 - CTD data for Bloukrans River RMT1x6 stations at sunrise and midday on the 25th and sunrise on the 26th October 1995.

DAY 1	TIME	DEPTH (M) AT EACH TIME			
	SUNRISE	6	11	22	27
	MIDDAY	6	14	23	34
Oxygen - umol.l^{-1}	SUNRISE	6.05	4.9	4.2	4.16
	MIDDAY	7.05	5.7	4.16	4.2
Nitrate - umol.l^{-1}	SUNRISE	4.76	12.1	17.8	20
	MIDDAY	0.25	10	17.9	17
Nitrite - umol.l^{-1}	SUNRISE	0.13	0.33	0.37	0.39
	MIDDAY	0.09	0.21	0.28	0.18
Silicate - umol.l^{-1}	SUNRISE	4.82	6.8	13.9	14.8
	MIDDAY	1.12	7.3	14.2	12.2
Phosphate - umol.l^{-1}	SUNRISE	0.85	1.3	1.52	1.65
	MIDDAY	0.52	1.49	1.22	1.1
Chlorophyll a - umol.l^{-1}	SUNRISE	4.1	9.2	0.15	1
	MIDDAY	1.1	1.92	0.78	0.3
DAY 2 - SUNRISE	DEPTH (M)				
	0	11	21	33	52
Oxygen - umol.l^{-1}	5.7	4.2	4.2	4.2	4.2
Nitrate - umol.l^{-1}	12	18.8	17.9	18.8	18.8
Nitrite - umol.l^{-1}	0.23	0.38	0.38	0.31	0.28
Silicate - umol.l^{-1}	7.8	14.1	14.1	14.1	14.7
Phosphate - umol.l^{-1}	1	1.48	1.61	1.48	1.48
Chlorophyll a - umol.l^{-1}	4.31	0.21	0.11	0.08	0.08

Larval distributions

On day 1, *E. whiteheadi* larvae were evenly distributed throughout the water column with the highest concentrations being caught at midnight (Table 6.4). The pattern on day 2 was very different, with larvae only found in the deep layer at sunrise and sunset and at the surface at sunrise, and with concentrations lower than observed the previous day. Although the concentration at the surface on day 2 was found to be significantly different from the other layers (F, 14.402; $P < 0.001$), the limited data base must again be considered when interpreting any statistical results in this section. Although mean sizes were different among the layers on the separate days, these differences were not significant. Size data combined from both days showed a trend of middle > surface > bottom, and sunset > sunrise > midnight, although differences were again not significant.

Merluccius capensis larvae were evenly distributed at sunrise and midday on the first day, but were only found in the bottom layer during later samples (Table 6.4). The low concentrations made it difficult to determine whether this was evidence of a downward movement during the night, as there were no statistical differences detected in distribution over time or depth. The same applied to samples from day 2 (Table 6.4), although most of the larvae were again concentrated in the deepest layer at night. Mean larval size on day 1 was equal between depths, while on day 2 there were significantly larger larvae occupying the deep station (F, 15.747; $P < 0.05$). No differences were detected with respect to size of larvae and different depths and times from both days combined.

Paracallionymus costatus displayed two very different distributional patterns on each of the sample days (Table 6.4). Low concentrations ensured that differences were not significant, but the majority of larvae were found in the lower two levels on day 1, being represented at the surface only at midday. All specimens on day 2 (Table 6.4) were caught at sunset and midnight in the deep water. Combining the data from each day revealed that while concentrations were greatest in the deep, the difference was not significant. In terms of larval size, there was no difference between samples from different depths on day 1 (larvae were only caught in deep water on day 2). Size data combined from both days revealed significantly larger larvae from deeper water compared to the middle layer (F, 9.336; $P < 0.01$).

Table 6.4 shows that larvae of Gobiidae Species 1 were caught at all times in the middle layer on day 1, but were absent at sunrise in the deep and at all times except sunset at the surface. The

difference in catches between the depth strata were not significant. On day 2, sunset again produced the most larvae, but this time none were caught in the deep, none were caught at sunrise and the only midnight representatives were found in surface samples (Table 6.4). Due most likely to the low densities, distribution over depth was again not found to differ significantly, even when both days' data were combined.

Gobiidae Species 2 larvae were absent from sunset and surface layer samples on day 1 (Table 6.4), with concentrations in the middle layer ($F_{.}$ 8.407; $P < 0.05$) being significantly greater than at other depths. On day 2, larvae were present in all three layers but at different times (Table 6.4). Low concentrations meant that no significant spatial differences could be detected. This was also the case for combined data from both days.

On day 1, Gobiidae Species 3 was present in all samples from the deep and midnight, with specimens also featuring in the middle layer at midday and sunset (Table 6.4). There were no detectable significant differences between densities at various depths. On the second day larvae were absent from all depths and all times except for midnight in the deep water (Table 6.4). This low incidence may be a reflection of patchiness rather than a preferred depth selection, and exposes the dangers of a restricted sampling regime. Looking at both days, the larger proportion of larvae were caught in the surface layer, but again this was not significant.

While overall trends were for larger larvae from the deepest layer for Species 1 and 2, and from the surface in Species 3, mean larval size did not differ significantly between catches from different depths, either on separate days or when all data was pooled.

Cynoglossus zanzibarensis larvae were absent from the deep layer on day 1 until sunset, and with the exception of midday in the middle layer, were present at all other times in the top two layers (Table 6.4). Although the trend was surface- and midnight-dominated, the differences between levels were not significant. On day 2 larvae were less prevalent, with specimens encountered in the deep and surface layer at sunset and at the surface only at midnight (Table 6.4). Perhaps due to the low concentrations, this unbalanced distribution was found to be significant, with greater densities being found at the surface ($F_{.}$ 7.981; $P < 0.05$). The dominance of the surface layer in terms of densities was also seen as highly significant ($F_{.}$ 7.014; $P < 0.001$) when data from both days was combined. The mean size of larvae was significantly greater in the deep water compared to both the middle and surface on day 1 ($F_{.}$ 6.945; $P < 0.01$) and to the surface on day 2

(F, 10.541; $P < 0.05$). Data pooled from both days revealed a significant difference between the larger deep water larvae and smaller surface caught larvae (F, 5.432; $P < 0.05$).

Austroglossus pectoralis seemed to have no clear pattern of distribution on day 1, with larvae being caught at all three depths (Table 6.4). On day 2 no larvae were caught in the deepest layer and none were caught at sunset. A few came from midnight samples in the surface layer, but most were caught in the middle and top layers at sunrise in similar densities (Table 6.4). A combination of the two days showed that surface densities were significantly higher (F, 4.132; $P < 0.05$). On the second day mean size was significantly larger in the middle layer (F, 70.683; $P < 0.01$) compared to surface caught fish. With sizes pooled from both days, no detectable differences were observed.

A look at total larvae showed very similar distribution patterns over time at all three depths on day 1 (Table 6.4), with no detectable significant differences. Apart from marginally higher densities at sunset on day 2, distribution was again very similar over all depths at all times (Table 6.4), with the sunset surface values not sufficient to detract from an overall homogeneous trend on the second day. A general trend in larval distribution was that concentrations were surface > bottom > middle. An interesting trend with respect to larval sizes is that the mean size of all larvae caught was significantly greater in the deep water when compared to both the middle and surface layers.

Egg concentrations were significantly higher in surface waters over both days (Table 6.4), but were present to varying degrees at all times in all depths. The lack of identification to species level complicates this picture as eggs often have species-specific characters with regards to density and buoyancy. Nevertheless, with data from both days the trend for surface dominance was clear (F, 13.325; $P < 0.001$).

Squid para-larvae were scarce in catches, appearing mostly as single specimens at various times of the day. As such, statistical tests for distributional trends were inappropriate. None were encountered in the surface waters on either day (Table 6.4), with most coming from the deep layer. Pooled size data from the two days revealed a trend of larger larvae from the deepest layer and from sunset, although low numbers meant that further statistical analysis was not feasible.

Larval distribution and the physical and biotic environment

Simple regression of the physical parameters obtained from the CTD rosette sampler and the temperature probe, and the measured plankton volume per sample, against overall egg and larval concentrations, revealed a poor relationship in all cases. The descriptive models and R^2 values for both voyages are presented in Table 6.6. The best relationships were obtained for total eggs and total larvae, with R^2 values of 34.23% and 37.87% respectively.

Table 6.6 - Descriptive models from the simple regression of physical and biotic parameters against total larval and egg concentrations from data collected between 7 and 8 October 1995 during R.S. *Africana* voyage #131 and 25 and 26 April 1996 during R.S. *Africana* voyage #135. Units of measurement were as follows: for larval and egg concentrations - #/m³, water temperature - °C, plankton - cm³, and all nutrients & oxygen - µmol.l^{-1}.

Independent Variable	Dependant Variable	Model	R^2 (%)
Voyage #131			
Chlorophyll-a	Total larval concentration	Y = exp(-1.727 + 1.014X)	7.07
Water temperature	Total larval concentration	Y = -11.409*X^3.654	6.14
Phosphate	Total larval concentration	1/Y = 6.292 - 1.249X	0.43
Oxygen	Total larval concentration	Y = -4.199*X^1.885	1.12
Silicate	Total larval concentration	Y = 0.765 - 0.039X	0.8
Nitrite	Total larval concentration	Y = -2.051*X^-0.482	5.05
Nitrate	Total larval concentration	Y = -0.843*X^-0.319	5.32
Plankton volume	Total larval concentration	Y = -3.356*X^0.823	37.87
Plankton volume	Total egg concentration	Y = -0.944*X^0.707	34.23
Plankton volume	*E. japonicus* egg concentration	Y = -1.583*X^0.608	9.46
Voyage #135			
Chlorophyll-a	Total larval concentration	Y = -2.492*X^0.180	10.82
Water temperature	Total larval concentration	Y = -0.027 + 0.01X	14.96
Phosphate	Total larval concentration	Y = 0.141 - 0.037X	5.28
Oxygen	Total larval concentration	Y = -0.034 + 0.026X	9.97
Silicate	Total larval concentration	Y = 0.135 - 3.884X	8.9
Nitrite	Total larval concentration	1/Y = 21.375 - 22.481X	5.14
Nitrate	Total larval concentration	Y = 0.141 - 3.381X	13.56

DISCUSSION

The vertical distribution of ichthyoplankton in the neritic region is an area of study which has not received much attention in southern Africa. References to species specific vertical stratification along the west coast and off Namibia by Olivar & Fortuño (1991) and the numerous works upon which their compilation is based (e.g. Olivar & Rubiés 1983, 1987; Olivar 1990) are vague and for the most part on a scale from 25 metre deep strata to ones in excess of 100 metres. Distribution

was more often described in terms of presence between particular isobaths rather than in definitive depth intervals. Discrete depth work on the eastern Agulhas Bank (Beckley 1994) dealt with patterns of certain species (*E. japonicus*, *S. sagax*, *E. whiteheadi*, *T. t. capensis* & *P. costatus*) and families (Cynoglossidae, Soleidae, Myctophidae & Sparidae) which were dominant (> 3%) in catches. Depth intervals varied from 10 metres at the surface up to 100 metres in the deepest strata. Within the Tsitsikamma National Park (TNP), Tilney & Buxton (1994) and Tilney *et al.* (1996) investigated the vertical distribution of the four most dominant families in the ichthyoplankton assemblage, namely the Gobiesocidae, Blenniidae, Engraulidae and Sparidae, by comparing their relative densities caught near the surface (1 - 3 m) and at approximately 15 m depth at inshore stations in 20 metres of water. While this present study dealt with distributional patterns at the species level, the depth strata sampled were governed by mechanical problems with the RMT1x6 net such that only meso-scale, and not micro-scale, patterns could be studied.

Not all marine fish larvae utilise a diurnal migration strategy. Discrete depth sampling using a BIONESS multiple net sampler off Peru (Sameoto 1982) showed that certain dominant species from the assemblage exhibited different behavioural patterns. While species such as *Leuroglossus stilbius*, *Bathylagus nigreys*, *Diogenichthys laternatus* and Malanostomiatidae species were confined to deepwater during daylight and surface waters at night, others such as *Merluccius gayi* were confined mostly to the surface at all times with only a few larvae at extreme depths. A third pattern of all larvae being found in surface waters all the time was observed for *S. sagax* and *Engraulis ringens*, illustrating that while conditions were the same for all species, the way in which each reacts to derive maximum benefit is species specific.

Several of the species which proved to be dominant in catches during both R.S. *Africana* voyages have previously been investigated with respect to their vertical distribution, both in southern African waters and in the case of *S. sagax*, off the west coast of Peru and California.

The three clupeiform larvae of *S. sagax*, *E. whiteheadi* and *E. japonicus* were found to be concentrated in the upper 25 metres of the water column off the coast of Namibia (Olivar 1990). Over the eastern Agulhas Bank, highest concentrations of *E. japonicus* and *S. sagax* were found in surface waters above the thermocline (Beckley 1994), while *E. whiteheadi* larvae were found in low densities throughout the water column. While no *E. japonicus* larvae were caught during either voyage in this study, the distribution of their eggs both inshore and offshore during voyage

#131 was even throughout the water column, with slightly higher densities being encountered in the surface layers. In this study, *E. whiteheadi* larvae were mostly found in similar densities at all depths, with the only significant difference being in greater densities in the surface layer above the thermocline on day 2 of voyage #135. There was also no apparent depth selectivity for *E. whiteheadi* larvae at different stages of development. During voyage #131, *S. sagax* larvae avoided the surface layer inshore and were concentrated mostly in the middle layer in the absence of a thermocline, while offshore they were found in all layers with the majority being concentrated in the middle layer which incorporated the top section of the deep thermocline. With the exception of larger *S. sagax* larvae in the deep layer from offshore sites on the second day of voyage #131, mean *S. sagax* size was equal throughout the water column. In a survey off the coast of Peru (Sameoto 1982) *S. sagax* showed no diurnal migratory behaviour and larvae from all developmental stages were found in the upper 30 metres (with a mode of 20 m) at all times. Off the Californian west coast, *S. sagax* was found to occur most frequently in the midwater, followed by the surface layer with the least found near the bottom (Watson 1992). This pattern applied to all stages, but early stages were less common than the later flexion and postflexion stages in both neuston and epibenthic layers. In terms of densities, yolk-sac and preflexion larvae were most prevalent in midwater and surface waters, and recently hatched individuals were rare near the bottom. Late stages were more homogeneously distributed with a slight trend of being more common in higher layers as distance offshore increased (Watson *op. cit.*).

Although the larvae of *Merluccius capensis* were found at all depths in this study there appeared to be a preference for the middle and deep layers. While the mean size of larvae was greatest in the deep layer on one occasion, in terms of developmental stages, there was an even distribution throughout. In the Benguela system, larvae and eggs of *M. capensis* have been found mainly over the 150 m isobath but also from the 125 - 350m isobaths, with the majority from the surface layer down to 200 m with maximum concentrations between 20 and 150 metres (Olivar & Rubiés 1987; Olivar 1990; Olivar, Rubiés & Salat 1992). A direct comparison with this study is difficult due to the different depth regimes mentioned for the Benguela. The avoidance of surface waters may, however, indicate a similar behaviour. A different pattern was observed for *Merluccius gayi* off the Peruvian coast during a survey in 1978 (Sameoto 1982) where most larvae were encountered above 30 metres at all times, although the deep presence still prevailed with some also being caught at 90 metres during the day. *Merluccius bilinearis* also appears to occupy

sub-surface layers in the Middle Atlantic Bight, with most larvae at 30 m during the day and shallower (15 m) at night, due either to avoidance at the shallower depth during the day or upward migration after dark (Kendall & Naplin 1981). An avoidance of the surface layer was also evident in *Merluccius productus*, which is known to spawn in mid-water over the continental slope in waters 150 - 500 metres deep. Their recently hatched larvae were found to congregate in or immediately beneath the mixed layer above the thermocline (Bailey, Francis & Stevens 1982).

Larvae of *T. t. capensis* were only caught during voyage #131 at the offshore stations from all three depth strata. Although the largest concentrations were observed from the middle layer, numbers were not sufficient to make it significant. The mean size of larvae was larger in the deeper waters on day 1 but equal between depths when size data from both days was combined. Eggs and larvae of *T. t. capensis* sampled in the Benguela system occurred from close inshore to over the continental slope (Olivar & Rubiés 1983) with maximum concentrations in the upper 50 m. On the east coast their distribution was mostly confined to the surface waters between 0 and 20 metres (Beckley 1994). The middle layer sampled at offshore stations during voyage #131, where highest concentrations of *T. t. capensis* larvae were found in this study, was between 10.6 and 45 metres. The inability to sample smaller depth increments meant that it was not possible to determine whether the middle layer larvae were contained above the 20 metre mark in this layer or below. The capture of *T. t. capensis* larvae at other times with the standard bongo sampling gear (see Chapter 5) meant that these larvae would have come from somewhere between 0 and 18.5 m. Exceptionally high concentrations in August of 1993 (0.96/m^3 at Middlebank and 0.41/m^3 for all stations combined) appear to support the findings of Beckley (*op. cit.*). However, the inability to sample beneath 18.5 metres on those occasions means that the complete vertical distributional picture remains unclear.

The distributional pattern of *P. costatus* larvae over the eastern Agulhas Bank differs to the one observed here. They were found to be widely distributed with no apparent preference for any particular depth (Beckley 1994), as opposed to an apparent preference for the middle and deep layers in this study. During both voyages the mean size of larvae in the deep layers was larger than those in the middle layer, although whether this was a function of a preferred depth for the later stages or reduced avoidance at that depth due to lower light intensity and low temperatures is not known.

A good indication of the lack of data for ichthyoplankton in the study area was revealed in the vertical distribution study by Beckley (1994). The Cynoglossidae sampled by Beckley (*op. cit.*) were treated as a single group, but were most likely a mixture of *C. capensis* and *C. zanzibarensis*, each with their own distributional characteristics. The lack of sufficient data means that Beckley's work and this study must be regarded as preliminary studies upon which further detailed work can be based. The cynoglossids sampled by Beckley (*op. cit.*) were found at all depths, with a maximum concentration from the 20 to 40 metre depth stratum, a region seemingly also favoured by the group Soleidae. The cynoglossids caught during this part of the study were mostly *C. zanzibarensis*. At both inshore and offshore stations during voyage #131 larvae of *C. zanzibarensis* appeared to avoid the surface layer, being found at maximum concentrations somewhere between 17.5 and 45 metres, a similar result to the pattern observed by Beckley (*op. cit.*). The pattern during the second voyage was, however, different to this with larvae being found in all three layers but predominantly in the surface layer (0 - 10.6 m). No reference to size distribution throughout the water column could be found in previous works. In this study the mean size of larvae was equal over depth for the first voyage, while significantly larger larvae were found at depth compared to the surface during voyage #135.

The scale of vertical stratification used in a study can also have far reaching influences on the interpretation of the results. For example, initial studies in the region of Shelikof Strait in the Gulf of Alaska showed that larvae of *Theragra chalcogramma* were mostly situated between 10 and 50 metres, but closer inspection revealed a migration to the top of this layer around sunrise and sunset, congregation in the deeper section during the day, and homogeneous distribution at night (Kendall, Clarke, Yoklavich & Boehlert 1987; Kendall & Kim 1989). A later study on the same species in the same area (Kendall *et al.* 1994) revealed a similar pattern, except larvae were deepest at sunrise, but also showed that while larvae were mostly confined to the upper 50 metres where prey was abundant, there was day to day variation with respect to depth distribution and the extent of vertical migrations.

Larvae of all sizes of *Pomatomus saltatrix* were found in the surface waters only off the coast of Catalan in the western Mediterranean (Sabatés & Martin 1993) during the peak summer spawning period. This distribution was attributed to the thermal profile of the water column, which was uniform down to 10 metres before a sharp temperature drop indicated a thermocline down to

30 metres. These findings provide credence to the premise that plankton distribution is spatially heterogenous, and one should design the sampling strategy around the physiochemical and biological structure of the sample area, e.g. in an area where a thermocline is present, plankton assemblages may differ above and below it rather than at discrete depths (Omori & Ikeda 1984b). While many species of fish have larvae which may be associated with surface and deep layers (Shenker 1988; Brodeur 1989), some are either entirely or mostly found in the neustonic layer (Doyle 1992; Doyle, Rugen & Brodeur 1995). There they are able to take advantage of peak copepod nauplii production in summer and, when larger, the wide variety of prey organisms in their lower densities in autumn and winter. In the western Gulf of Alaska, larvae of certain species are regarded as obligative neuston dwellers despite the adults being demersal spawners. These include members of the Hexagrammidae, Cottidae, *Anoploma fimbria* and *Cryptacanthodes aleutensis*. Other species, such as *Theragra chalcogramma, Ammodytes hexapterus* and *Bathymaster* spp., have been classified as facultative neuston inhabitants which undergo diel migrations to the surface at dusk to take advantage of a favourable feeding regime and return to the depths during the day. Amongst *A. hexapterus* and *Bathymaster* spp., however, there appears to be a size threshold below which larvae migrate downward at night. It is only the larger specimens which exhibit this facultative neuston behaviour. It has been proposed (see Yamashita, Kitagawa & Aoyama 1985) that the smaller larvae exhibit a diurnal feeding pattern at the surface and use the night-time migration to the depths as a predator avoidance mechanism.

Although there are a host of vertical distribution combinations, a general trend particularly amongst tropical fauna, known as a Type I migration, is that larvae migrate to surface waters at night and return to deeper waters during times of intense photoperiod (see Ahlstrom 1959; Neilson & Perry 1990). Even in some studies where maximum concentrations of larvae at night are recorded from mid-layers, e.g. Boehlert *et al.* (1992), the authors expressed reservations as the surface layer or neuston was undersampled. Nevertheless, in their study as well as others (Loeb 1979; Sameoto 1986) peak planktonic concentrations are often coincidental with the depth of the thermocline, implying that temperature is a primary causal factor in vertical larval patterns. The Type II migration pattern, where larvae migrate into deeper waters at night and occupy surface layers during daylight hours, is less common but has been observed for several species (Boehlert, Gadomski & Mundy 1985; Yamashita, Kitagawa & Aoyama 1985; North & Murray 1992; and others in Brodeur & Rugen 1994). Another generalisation with respect to vertical distribution is

that early stages such as yolk-sac and preflexion larvae are found in surface layers, either due to buoyancy of eggs or near-surface spawning behaviour, as has been observed for certain sparids (see Buxton & Garratt 1990). The later staged flexion and postflexion individuals are then found deeper (Loeb *op. cit.*; Castonguay & McCleave 1987; Boehlert *et al.* 1992), although exceptions to this occur frequently enough to cast some doubt as to this being the most common pattern. An additional reason for the occurrence of young stages near the surface was proposed by Lenarz *et al.* (1991) for the rockfish *Sebastes paucispinis* in the California Current. Relative to co-occurring *Sebastes* species, larvae of *S. paucispinis* grew rapidly and needed the higher temperatures and food densities encountered in the surface layer.

In a study off the west coast of Peru, Sameoto (1982) demonstrated that there was a significant linear relationship between the total number of larvae per unit area and the zooplankton biomass, but no relationship between individual species and zooplankton biomass. The relationship between settled plankton volume and ichthyoplankton in the TNP between January 1991 and July 1992 (Tilney & Buxton 1994) was first considered to be poor, but once unusually large catches of engraulid larvae in January 1991 had been removed from the analysis the significant plankton-larvae relationship (R^2 - 81.5%) suggested a link between larval survival and plankton volume. Although the general appearance in this study seemed to be increased larval densities with greater plankton volume, the relationship was weak (R^2 = 37.87 & 34.23% for larvae and eggs respectively - see Table 6.6). However, the short time span involved here may have affected this result and masked the true pattern which may well be the one observed by Tilney & Buxton (*op. cit.*). There is an alternative view which finds low larval concentrations amongst high densities of plankton not surprising, as fish larvae are rare amongst the zooplankton community (McGowan & Miller 1980) and must often compete for food and space and contend with numerous predators. Although not quantified, many samples during this section of the study as well as over the rest of the period contained high densities of chaetognaths which are probable predators of fish larvae (Lebour 1923; Williams & Hart 1974). On two separate occasions, Gobiidae Species 2 larvae were found engulfed by these arrow worms. However, whether the larvae were co-occurring with these predators could not be determined as the depths sampled were usually extensive and micro-scale distributions could not be ascertained.

Nutrients such as nitrate, silicate and phosphate exhibit strong regional differences in concentrations over the Agulhas Bank (Lutjeharms, Meyer, Ansorge, Eagle & Orren 1996). Historical data collated from research voyages over the Agulhas Bank between 1925 and 1985 revealed that levels of silicate and phosphate at the surface on the eastern Agulhas Bank were generally low at <1.0 $\mu mol.l^{-1}$ and < 0.5 $\mu mol.l^{-1}$ respectively. However, close inshore and in the vicinity of coastal headlands such as Algoa Bay, Cape St Francis, and Plettenberg Bay values were higher. Nitrate, the limiting nutrient in most oceanic waters, reached values between 5 $\mu mol.l^{-1}$ and 25 $\mu mol.l^{-1}$ close to shore in the TNP region. Nutrient values on the western Agulhas Bank tend to increase with depth (Lutjeharms *et al. op. cit.*). This trend is followed on the eastern Agulhas Bank region for both silicate and phosphate, but nitrate appeared to decrease with depth in the nearshore to values < 5 $\mu mol.l^{-1}$. Trends and values extracted from historical data indicate that subtropical surface water is the source for the surface waters over the eastern Agulhas Bank as the range of nutrient values are very similar (Goschen & Schumann 1988). Seasonal data collected between 1974 and 1979 indicated that surface waters in the euphotic zone above the spring/summer thermocline were nutrient poor as a result of primary production (Lutjeharms *et al. op. cit.*). In winter, however, extensive mixing erodes the thermocline and nutricline layer and brings deep nutrient rich waters to the surface.

Values obtained from this study showed a great deal of variation when compared to the long term trends observed in Lutjeharms *et al.* (1996). Inshore stations from voyage #131 revealed nitrate values which were considerably lower than the nearshore values from historical data. Phosphate values seemed to conform to an expected < 0.5 $\mu mol.l^{-1}$, but silicate values exceeded the expected. The reason for the observed deviations could be that the inshore stations in this study were closer to the shoreline than the sites sampled before, and as such are most likely not a part of the historically sampled area. While values most certainly varied with depth, the trend was not always one of increase and on occasion values decreased in the mid-water before showing signs of increasing again. The pattern offshore during voyage #131 was more akin to expected trends based on historical data with low values in surface and sub-surface waters before increases through and below the thermocline. Variation over a 24 hour period was also quite extensive. The nutrient values obtained for voyage #135 displayed similar trends to those observed during voyage #131, except that surface values were generally higher and maximum values were attained at shallower

depths (see Table 6.5), most likely due to the well defined, shallow thermocline which had intruded into surface waters.

Productivity in the geographic region which incorporates the study area was alluded to by Beckley (1994) who stated that large phytoplankton cells over the eastern Agulhas Bank ensured a highly variable distribution of chlorophyll-a. The high levels of 2 - 5 µg/l recorded by Beckley (*op. cit.*) were associated with the thermocline in sub-surface layers. Similarly, chlorophyll-a levels measured during this study showed surface or sub-surface maxima above or just within the thermocline which declined rapidly through this cold water layer. The timing of sampling in October 1995 as opposed to April 1996 for the respective voyages and their corresponding deep and gradual, and shallow and defined thermoclines may have had some bearing on these chlorophyll-a readings. During voyage #135, the colder nutrient rich waters were closer to the surface and hence the photic zone which is a primary requirement for the production cycle.

The lack of any concrete relationships between larval concentrations and elements such as chlorophyll-a, nitrate, phosphate and silicate in this study may be a reflection of the limited data base. Having said this, however, the possibility that species specific patterns have been masked by grouping all larvae together is recognised. It was felt that due to the general diffuse nature of their distribution and the low densities, any relationships between individual species and environmental factors would have been meaningless. The most likely explanation is that larval distribution is not determined by any one variable and that each species must weigh the options of environmental comfort and biological interaction with food and predators to ultimately decide on their preferred vertical placement at any one time. Neilson & Perry (1990) echoed this sentiment in a review paper by stating that the wide range of vertical migration patterns observed for larval fish is indicative of a facultative process dictated by multiple environmental factors. During larval surveys between Point Conception and San Diego in the southern California Bight (Brewer, Lavenberg & McGowen 1981) no significant correlation could be found between larval abundance and chlorophyll-a or zooplankton concentrations, for an assemblage which comprised a variety of species, including *Scomber japonicus*. When larvae of a particular species are present in sufficient densities and with a reasonable frequency in catches it is possible to discern relationships with certain physical factors. For example, with respect to primary production. Sameoto (1982) found that *Engraulis ringens* larvae off the coast of Peru were the only ones within the assemblage with a detectable relationship

between concentration and chlorophyll-a levels, with highest densities of larvae being found at stations where chlorophyll-a levels were between 9 and 12 mg/m^3. Pulses in chlorophyll-a production occur on a regular basis in spring in the region of the Derwent Estuary in Tasmania where larvae of the blenny, *Parablennius tasmanianus tasmanianus* abound. However, despite a prolonged planktonic stage of approximately 46 days (Chamchang 1997) also in spring, no consistent relationship between chlorophyll-a pulses and larval abundance, hatching times or settlement could be found.

On a large to meso-scale, the patchy nature of ichthyoplankton distribution may be the result of living in a fluid and dynamic pelagic environment where gradual spatial variation amongst species can be expected (Doyle *et al.* 1993). On a smaller scale, however, one may expect sharply defined boundaries such as thermoclines and pycnoclines, and certain current regimes to influence distribution such that distinct concentrations of larvae reflect the spatial structure of certain oceanographic features and physical parameters. In stratified waters, most larvae are generally found above or in the thermocline (Ahlstrom 1959; Olivar & Sabatés 1997) which has been viewed as an interface for interactions between fish larvae and zooplankton as well as a barrier to vertical migration (Davis et al. 1990). Not all authors concur with this statement, with Gray (1996) stating that in a study off south-eastern Australia "... vertical trends in numbers of taxa and individuals were generally not related to the position of the thermocline." Gray (*op. cit.*) did find that many larvae were most abundant in certain depth zones, with their positioning near the surface, mid-water and bottom layer being species specific irrespective of the presence or absence of a thermocline. In contrast, Olivar & Sabatés (*op. cit.*) found most fish larvae in the north-west Mediterranean were located above the thermocline, with a large overlap in vertical distribution between species. In particular, the sparids *Boops boops* and *Diplodus sargus*, the serranid *Serranus hepatus*, and the anchovy *Engraulis encrasicolus* were most abundant in surface waters. While *Arnoglossus* sp. and *T. t. capensis* were found from the surface through the thermocline, only *Callionymus* species and gobiids were well represented beneath the thermocline. In an earlier study, Gray (1993) even found differences in vertical distribution between taxa which were sampled above the thermocline. No sampling was performed beneath the thermocline, demonstrating how important stratified sampling is to fully understand coastal larval community dynamics. Preferable positions in the water column appear to be taxon specific, with some groups showing a higher degree of elasticity than others. For example, Gray (1993) showed that in waters

off New South Wales. Myctophidae and Triglidae were more abundant at depth. Cheilodactylidae and *Gonorhynchus greyi* larvae were more surface oriented. and Anthiinae and Sparidae (*Acanthopagrus australis*) larvae were equally distributed throughout. Furthermore. members of the Bothidae were more abundant at depth at most stations. but were found in similar concentrations at all depths at a few sites. The differences in preference between taxa means that in distributional studies. each species must be considered on its own merit instead of viewing the species assemblage as a whole. Although random diffusion or passive larval transport may partly explain the patchy nature of ichthyoplankton. the vertical distribution as a result of behaviour and preferences for certain conditions may be equally important. The extent to which physical parameters such as currents and nutrient levels were observed to change over small spatial and temporal scales makes it difficult to generalise about the observed distribution of larvae. The chances of the physical environment differing quite extensively outside the region of the sample sites cannot be ruled out. Although no relationships could be found between the vertical positioning of larvae and certain physical parameters in this study. there may be a more complex interaction involved which is not yet understood. Unless further. more extensive and intensive sampling can be done. the vertical placement of larvae observed here can only be discussed in the context of the specific environmental conditions recorded on site. and in the context of a limited sampling regime and restricted data base. Any generalisations on species' preferences. unless backed up by specific references to them in the literature. would be out of context. Similarly. to surmise about species interactions would require sampling at smaller intervals of discrete depths (see Doyl *et al. op. cit.*; Gray 1993). as larvae may occupy positions in the water column on a microscale such that a > 10 metre wedge may be so large as to obscure the true picture (e.g. Kendall *et al.* 1987; Kendall & Kim 1989).

CHAPTER 7 - A PRELIMINARY APPRAISAL OF THE DISPERSAL POTENTIAL OF ICHTHYOPLANKTON FROM THE TSITSIKAMMA NATIONAL PARK

INTRODUCTION

Larval behaviour is linked to finding the optimal conditions for survival and may often be the result of a compromise between favourable physical conditions, food preferences and availability, and predator avoidance (Smith & Lasker 1978; Hunter 1981; Power 1986). Due to the dynamic nature of the ocean with respect to physical and biological conditions, the most likely scenario is that fish spawning grounds are located far from nursery and juvenile settlement areas (Harden-Jones 1968; Cushing 1986; Hare & Cowen 1993), as is the case for engraulid and clupeid species along the west coast of southern Africa (Armstrong & Thomas 1989). However, there is evidence of retention over or near some spawning grounds for species such as the Atlantic herring, *Clupea harengus* (Lauzier 1967; Tibbo & Lauzier 1970; Stobo, Hunt & Iles 1973; Bradford & Iles 1993), although in the North Sea larvae are dispersed eastwards from the spawning grounds (Clark 1933; Bückmann 1942 in Cushing *op. cit.*). In both cases, conditions should exist that would promote either active retention, or dispersal, of eggs and larvae if survival beyond the early developmental stages, and hence recruitment, is to be ensured. In the case of retention, ichthyoplankton may be retained in the immediate area of spawning for the entire period prior to settlement by, for example, tidal residual circulations. Alternately they may initially be transported away into a favourable environment before being returned to the spawning or settlement area towards the end of the larval stage, as happens with *C. harengus* over the Georges Bank (Iles & Sinclair 1982) by tidally induced anticyclonic gyres. If widespread dispersal is the mechanism used for recruitment and survival of the species, then from the moment of spawning the eggs and larvae are advected away (Leis & Miller 1976) from the point of origin by residual ocean currents and tidal streams.

In either case, the distribution of early stages and the success of dispersal or retention is ultimately controlled by both passive transport and active behaviour (Norcross & Shaw 1984). While the extent and direction of passive transport is largely determined by advective and diffusive oceanographic components (Power 1984; Hare & Cowen 1993), it may be enhanced or retarded by the behavioural actions mentioned above. Certain coral reef species exhibit

considerable control over the extent of their displacement through a combination of local, multidimensional circulation patterns, spawning mode and behaviour, and larval behaviour (Hamner, Jones, Carelton, Hauri & Williams 1988; Leis 1991, 1993). Even during the egg stages, differential buoyancy and density properties can result in different magnitudes of dispersal or retention. The chief mechanism responsible for the transport of fish eggs and larvae are the oceans' currents (Leis & Goldman 1983) that, in the nearshore zone, may be induced by winds (Eckman transport), geostrophic phenomena, coastal trapped waves or tidal flows (Bishai 1959; Bailey 1981; Hewitt & Methot 1982; Norcross & Shaw *op. cit.*). The reliance by certain fish species on specific transport regimes to attain the appropriate habitat for larval survival or later settlement means that variation or deterioration of the desired feature could lead to mass mortality and poor recruitment (Parrish, Nelson & Bakun 1981; Hare & Cowen 1993). *Engraulis japonicus* provides a good example of a species which relies on a shelf-edge frontal jet to transport larvae from the summer spawning site around the Cape of Good Hope to the nursery area off Lamberts Bay up the west coast of South Africa (Shelton & Hutchings 1981). Spawning itself does not seem to rely on the presence of this frontal jet, so its absence means that larvae will be stranded on the spawning grounds resulting in failed recruitment further north. In order to cope with mortalities in a dynamic and often unpredictable environment, many coastal species have been shown to increase their reproductive potential with high fecundities, protracted spawning seasons and numerous spawning sites (Garrod & Knights 1979 in Norcross & Shaw *op. cit.*).

It is widely accepted that the majority of marine larvae are dispersed by what is called planktonic drift (Marliave 1986), and that this drift plays an important role in larval ecology (Smith 1972; Power 1986). In addition to ensuring dispersal, it is recognised that pelagic larvae provide the potential for recovery or recolonisation of an environmentally degraded area. While this may refer to areas damaged by storms or pollution, it can also be taken to include over-exploited fishing grounds where populations are too small to be self sustaining. It is this potential source of planktonic larvae, originating from within the boundaries of Marine Protected Areas (MPA's) such as the Tsitsikamma National Park (TNP) that is of concern here.

The TNP has been shown to be an effective conservation option for resident populations of reef fish species such as sparids (Buxton and Smale 1989). However, the effectiveness of a marine

reserve should not only be judged by the protection it affords resident fishes, but also in terms of the effect it has on fish populations beyond its boundaries, through the export of adults, juveniles, eggs and larvae. Along the east coast of South Africa, reef fishes constitute a significant proportion of the commercial and recreational linefishery and spearfishery catches each year (Penney *et al.* 1989; Brouwer, Mann, Lamberth, Sauer & Erasmus 1997; Mann, Scott, Mann-Lang, Brouwer, Lamberth, Sauer & Erasmus 1997). Key reef species like *Chrysoblephus laticeps* and *C. cristiceps* are stenotopic, and any migration by juveniles and adults to areas adjacent to the reserve is thought to be insignificant (Buxton & Allen 1989). However, many of these species have a pelagic phase to their life cycle. The adults are broadcast spawners that leave the confines of the reef to release large numbers of eggs and sperm in the upper reaches of the water column, e.g. *C. laticeps* and *Cheimerius nufar* (Buxton 1990; Buxton & Garratt 1990) . According to the herring hypothesis (Iles & Sinclair 1982) and the member/vagrant hypothesis (Sinclair 1988), the majority of these eggs and larvae may be retained in the immediate vicinity of their home reef. Alternatively, they may be passively dispersed to regions distant from their origin by a number of physical factors as described in the match/mismatch theory (Hjort 1914; Cushing 1967, 1986). In contrast to the assumption by Harden-Jones (1968) that eggs and larvae drift passively to nursery areas, surveys have recently indicated that ichthyoplankton is retained close to the original spawning area, perhaps by tidally generated gyres (Gagne & O'Boyle 1984) in concurrence with the larval retention theory (Suthers & Frank 1989), where the same area acts as a spawning, nursery, and recruiting ground (Smith & Morse 1985). It would nevertheless appear that the pelagic component of the life cycle has the largest potential for dispersal into adjacent areas.

As pointed out by Tilney *et al.* (1996), the issue of ichthyoplankton dispersal from MPA's is a topic of early life history research that has been neglected, although the retention and dispersal of marine eggs and larvae *per se* have been extensively covered (e.g. Bishai 1959; Graham 1972; Nelson, Ingham & Schaaf 1977; Bailey 1981; Barlow 1981; Maxwell & Cresswell 1981; Melville-Smith *et al.* 1981; Fortier & Leggett 1982, 1983; Arnold & Cook 1984; Norcross & Shaw 1984; Power 1984; Beckley 1985, 1993; Smith & Morse 1985; Nelson & Hutchings 1987; Shanks 1988; Bergman, Veer, van der Stam & Zuidema 1989; Cushing 1990b; Hutchins & Pearce 1994; Champalbert & Koutsikopoulos 1995; Colin 1995; Koutsikopoulos, Dorel & Desaunay 1995). The aim of this section of work was to appraise the potential for dispersal or retention of ichthyoplankton which originates from within the protective boundaries of the TNP by

investigating local current patterns and larval distribution (see also Leis & Goldman 1983; Tilney *et al. op. cit.*). In so doing it was envisaged that the foundation could be laid for future work to concentrate on this aspect that should be seen as a vital function of MPA's in general. If the pelagic eggs and larvae originating from a particular spawning ground are dispersed, then the extent to which such dispersal from their point of origin takes place should define the locations of marine reserves in relation to local dispersal mechanisms as well as delimit the extent of their boundaries.

METHODS AND MATERIALS

Sample times and locations of the double-oblique bongo tows in the vicinity of the satellite tracked sub-surface canvas drogues are described in Chapter 1. To coincide with the depth at which the drogues were operating between the surface and 11 m, 40 metres of rope was used to ensure a maximum sampled depth of 10.3 ± 0.23 m (see Chapter 2 - Table 2.1). In all cases the tow path passed to within a few metres of the drogue at some stage during the sample so as to ensure that the eggs and larvae present in the samples came from the same body of water whose movements would be described by the drogues. Sample processing and identification followed the protocol outlined in Chapter 2. Based on the speed and direction of the currents indicated by the drogues, and the distance that the body of water covered over time, certain assumptions were made as to the dispersal of the ichthyoplankton which was sampled in the same vicinity.

Of the 57 drogues that were released only one, released at approximately 1 nautical mile (nm) offshore on July 23 1996, could not be used due to the loss of the satellite signals to the GPS some time after release. In order to work out drogue velocity, the number of minutes of latitude and longitude were calculated by simply subtracting the recovery reference points from the release references. While 1 minute of latitude is equivalent to 1 nautical mile (approximately 1.89 km), 1 minute of longitude is less than 1 nautical mile when one is not on the equator (Chamberlin 1950). It is reduced by a factor of cosine(latitude), which at the release point in the TNP is about 0.83.

Additional data concerning the current patterns in the TNP were obtained from the ADCP readings during the vertical distribution work on board the R.S. *Africana* (see Chapter 6), as well as from the literature (e.g. Schumann *et al.* 1982; Boyd & Shillington 1994; Tilney & Buxton 1994; Tilney *et al.* 1996). Dispersal potential of eggs and larvae are discussed in the

light of this information and with respect to behaviour and distributional patterns observed during the course of this study.

RESULTS

A total of 19 species of larvae were identified from the bongo samples (Table 7.1). Included amongst these were five representatives of the Sparidae, namely *A. argyrozona*, *C. laticeps*, *D. s. capensis*, *P. b. natalensis* and Species 11. In most cases larval abundance was low. In the July samples, *S. sagax* was present in the highest concentrations, whilst *E. japonicus* featured more prominently in October. The single *Z. faber* larva was recently hatched as it still showed remnants of the yolk-sac and, although the percentage of flexion and postflexion larvae was high amongst *S. sagax*, the majority of the remaining species were in the early preflexion stages of development. Other single specimens which were flexion or later stage included *L. hectoris*, *P. pilicornis*, Blenniidae Species 6, *Pomadasys olivaceum*, and *C. laticeps* (Table 7.1).

Drogues

The frequent longshore current reversals with a periodicity of anywhere between two and twenty days that were described in detail in Chapter 1 were clearly evident at times, as were periods of persistent uni-directional currents. From 11 to 13 April 1996 the longshore component of the currents close inshore was in a westerly direction (Table 7.2), gaining in momentum from 0.67 $m.s^{-1}$ on the first day to 2.51 $m.s^{-1}$ on the third. On the 14th and 15th, however, the longshore component was strong easterly both inshore and further offshore, with the fastest speeds being recorded from the inshore drogues at 4.74 $m.s^{-1}$ and 4.21 $m.s^{-1}$ for the respective days. For four days in July 1996, longshore currents were in a westerly direction with velocities ranging from 3.08 $m.s^{-1}$ to 5.17 $m.s^{-1}$. On the first three days during this period, the strongest currents were again inshore (Table 7.2). With the exception of two instances where a weak easterly current was detected, the period from 30 September to 4 October 1996 was also characterised by longshore westerlies, with the current on the 3rd and 4th registering the fastest velocities in the study at 7.03 $m.s^{-1}$ and 6.33 $m.s^{-1}$. Later that same month, on the 14th and 15th, the current had reversed to an easterly direction once again. A rapid reversal from easterly to westerly currents was observed during November 1996, with an easterly component ranging from 1.77 $m.s^{-1}$ to 2.36 $m.s^{-1}$ on the 11th and a westerly

Table 7.1 - Concentrations and sizes (BL) of fish larvae captured with bongo nets during drogue studies from July 1996 to October 1996 in the study area. The distance offshore (nautical miles) measures the release point off Storms River of the drogue around which tows were conducted (* flexion or post-flexion larvae).

Date	Distance Offshore (nm)	Species	Concentration (#/m^3)	Size (mm)
7/20/96	3.0	*Chelidonichthys capensis*	0.003227472	5.5
		Sparidae Sp11	0.003227472	4.0
		Zeus faber	0.003227472	3.3
		Engraulis japonicus	0.003227472	5.7
		Sardinops sagax	0.003227472	19.6*
	1.5	*Sardinops sagax*	0.028798526	13.1 - 19.7*
		Gobiidae Sp2	0.002879853	4.3
7/22/96	2.5	*Engraulis japonicus*	0.002768549	7.5
		Sardinops sagax	0.049833887	10.1 - 13.6 (55.5%*)
		Lampanyctodes hectoris	0.002768549	6.4*
		Parablennius pilicornis	0.002768549	5.6
		Blenniidae Sp7	0.002768549	5.5
		Pagellus bellotti natalensis	0.002768549	4.5
		Diplodus sargus capensis	0.002768549	4.7
		Paracaillionymus costatus	0.002768549	2.2
		Gaidropsarus capensis	0.002768549	3.4
		Chelidonichthys capensis	0.002768549	5.0
		Merluccius capensis	0.002768549	1.6
		Cheilodactylidae Species 1	0.002768549	4.5
	1.5	*Sardinops sagax*	0.011629935	9.2 - 15.5 (75%*)
		Engraulis japonicus	0.002907484	8.1
		Parablennius pilicornis	0.002907484	8.8*
		Blennidae Sp6	0.002907484	7.7*
		Diplodus sargus capensis	0.002907484	4.5
		Argyrozona argyrozona	0.002907484	3.3
		Gaidropsarus capensis	0.002907484	3.0
		Pomadasys olivaceum	0.002907484	6.1*
10/14/96	1.0	*Parablennius pilicornis*	0.00549179	5.9 - 6.0
		Sardinops sagax	0.002745895	17.9*
		Chrysoblephus laticeps	0.002745895	5.6*
10/15/96	1.0	*Engraulis japonicus*	0.014176354	2.4 - 4.2
	2.0	*Engraulis japonicus*	0.010564124	5.0 - 6.8
		Sardinops sagax	0.007042749	2.6 - 6.4
		Parablennius pilicornis	0.003521375	6.3
		Chrysoblephus laticeps	0.003521375	5.3
		Coccotropsis gymnoderma	0.003521375	3.0

component registering between 1.41 $m.s^{-1}$ and 1.92 $m.s^{-1}$ on the 12th. For three consecutive days in January 1997, longshore westerly currents prevailed at all stations, varying in strength from 1.86 $m.s^{-1}$ at an inshore site to 6.22 $m.s^{-1}$ just less than a nautical mile further offshore (Table 7.2). On the fourth day the pattern was reversed with easterly currents being detected at all stations ranging from 1.32 $m.s^{-1}$ offshore to 3.92 $m.s^{-1}$ inshore.

Using an average current reversal frequency of three days (72 hours) the potential distance which the bodies of water represented by the drogues could move, would range from as little as 0.47 km to as much as 182.25 km. The average distance over which a body of water could move over three days would be 81.27 ± 42.62 km.

From the sea surface temperature (SST) readings that were obtained at the site of release and recovery (Table 7.2) the only indication of upwelling was between the 11th and 13th April 1996. Over a 48 hour period the SST dropped from 15.5 (11th) to 10.5 (13th) after easterly winds of 10 to 15 knots. On the 12th and 13th of that month the drogue movement was south-westerly and offshore which conforms to the expected movement of the water body during upwelling events. For the most part, the frequent changes in wind direction, mostly from westerlies in the morning at times of release to easterlies in the afternoon when drogues were recovered (Table 7.2), made it difficult to relate on- or offshore displacement with wind-induced drift.

ADCP - discrete depth profiles

Inshore stations during voyage #131 (Figure 7.1) showed a predominantly easterly longshore component over both days that was strongest near the surface at 18 m ranging from 60.4 cm/s on day 1 to 56.2 cm/s on the second day. Currents were weaker in the deeper layers and considerably slower near to the bottom on the second day, registering only 3 cm/s and 6.4 cm/s at 26 and 34 metres respectively.

In the deeper waters of the offshore stations sampled during voyage #131, the current profile exhibited a wide range of velocities and vectors with depth. At 21h00 on day 1 (Figure 7.2a) a strong offshore component up to 47.1 cm/s was recorded down to 26 m. Currents then proceeded to spiral round to the east in the middle layers with decreasing strength (20.6 to 1.9 cm/s) before turning onshore at 66 metres at a moderate strength between 4.9 and 5.6 cm/s. By 23h00 (Figure 7.2b) the offshore component had weakened close to the surface and at 26 m had already swung to the west at 9.7 cm/s after which it first spiralled towards onshore and then back again to a weak west current of 6.8 cm/s at 74 m. By 01h00 (Figure 7.2c) the offshore component had been

Table 7.2 - Data on the release and recovery points of drogues, their drift, calculated current velocity and wind dircetion and speed at the time of drogue release and recovery within the study area over the period April 1996 to January 1997 (Ls - longshore; Os - onshore; Of - offshore; E - east, NE - north-east; ESE - east-south-east; SE - south-east; SW - south-west; W - west; VAR - variable; wind speed in knots; N/R - No reading; Sea Surface Temperature in °C).

	Release Site		Recovery Site		Time Adrift	Drift Direction		Current Velocity (m/s)		Wind Direction and Speed		Sea Surface Temperature	
Date	Latitude	Longitude	Latitude	Longitude	(Hours)	Ls	Os/Of	Ls	Os/Of	Release	Recovery	Release	Recovery
4/11/96	34.02.99	23.53.42	34.02.88	23.53.04	2.97	SW	Os	0.67	0.19	E, 10	E, 12	15.5	15.5
4/12/96	34.02.93	23.53.68	34.02.95	23.51.22	5.30	SW	Of	2.44	0.02	ESE, 14	E, 18	14.5	15.0
4/13/96	34.02.98	23.53.85	34.04.13	23.50.28	7.47	SW	Of	2.51	0.81	ESE, 15	E, 15	10.5	11.0
4/14/96	34.02.65	23.54.32	34.02.96	23.58.94	5.12	NE	Of	4.74	0.32	SW, 15	E, 2	11.5	11.2
	34.02.99	23.53.91	34.03.09	23.58.10	5.17	NE	Of	4.26	0.10	SW, 15	E, 2	11.5	11.2
	34.03.52	23.53.80	34.03.24	23.57.56	5.12	NE	Os	3.86	0.29	SW, 15	E, 2	11.0	11.2
	34.04.01	23.53.81	34.03.72	23.56.57	5.05	NE	Os	2.87	0.30	SW, 15	E, 2	11.0	11.2
4/15/96	34.02.50	23.54.13	34.03.27	23.59.44	6.62	NE	Of	4.21	0.61	W, 2	0	13.0	15.0
	34.03.00	23.54.02	34.03.84	23.53.88	6.58	NE	Of	3.88	0.67	W, 2	0	12.0	13.0
	34.03.46	23.53.99	34.04.44	23.58.33	6.43	NE	Of	3.54	0.80	W, 2	0	12.0	13.0
	34.04.07	23.54.11	34.05.30	23.56.86	6.30	NE	Of	2.29	1.03	W, 2	0	12.0	12.0
7/20/96	34.02.55	23.53.88	34.01.98	23.48.74	5.22	SW	Os	5.17	0.57	SW, 10	SW, 10	16.5	16.5
	34.03.03	23.53.86	34.02.18	23.49.19	4.98	SW	Os	4.92	0.90	SW, 10	SW, 10	16.4	16.5
	34.03.45	23.53.84	34.02.69	23.49.65	5.00	SW	Os	4.40	0.80	SW, 10	SW, 10	16.5	16.5
	34.04.11	23.53.86	34.03.44	23.50.72	5.23	SW	Os	3.15	0.67	SW, 10	SW, 10	16.5	16.5
7/21/96	34.02.53	23.53.72	34.01.78	23.49.59	5.85	SW	Os	3.71	0.67	W, <5	W, <5	16.0	16.5
	34.03.15	23.53.76	34.02.36	23.49.76	5.80	SW	Os	3.62	0.72	W, <5	W, <5	16.0	16.5
	34.03.47	23.53.82	34.02.67	23.50.46	5.73	SW	Os	3.08	0.73	W, <5	W, <5	16.5	16.5
7/22/96	34.02.61	23.53.75	34.01.98	23.48.31	6.45	SW	Os	4.43	0.51	VAR, <5	ESE, 20	16.0	16.3
	34.03.08	23.53.44	34.02.45	23.48.27	6.37	SW	Os	4.26	0.52	VAR, <5	ESE, 20	16.0	16.3
	34.04.13	23.53.74	34.02.79	23.49.24	6.47	SW	Os	3.65	1.09	E, <5	ESE, 20	16.0	16.3
7/23/96	34.02.51	23.53.93	34.02.25	23.48.54	5.63	SW	Os	5.02	0.24	E, 15	E, 30	16.0	15.7
	34.04.71	23.53.60	34.04.75	23.48.15	5.60	SW	Of	5.11	0.04	E, 20	E, 30	16.0	16.0
9/30/96	34.02.71	23.53.54	34.02.33	23.52.28	5.25	SW	Os	1.26	0.38	SW, <5	VAR, <5	16.0	15.7
	34.03.64	23.53.69	34.03.16	23.52.94	5.27	SW	Os	0.75	0.48	SW, <5	VAR, <5	18.0	19.0
	34.04.62	23.53.67	34.04.42	23.53.69	5.22	NE	Os	0.02	0.20	SW, <5	VAR, <5	18.0	18.5
	34.04.09	23.53.87	34.03.73	23.53.51	5.05	SW	Os	0.37	0.37	SW, <5	VAR, <5	18.0	18.0

Table 7.2 continued.

	Release Site		Recovery Site		Time Adrift	Drift Direction		Current Velocity (m/s)		Wind Direction and Speed		Sea Surface Temperature	
Date	Latitude	Longitude	Latitude	Longitude	(Houre)	La	Os/Of	La	Os/Of	Release	Recovery	Release	Recovery
10/2/96	34.02.50	23.53.85	34.02.07	23.53.87	5.80	NE	Os	0.02	0.39	SW, 15	SW, 10	N/R	18.0
	34.03.50	23.53.85	34.03.23	23.52.12	6.10	SW	Os	1.49	0.23	SW, 15	SW, 10	N/R	17.5
10/3/96	34.02.50	23.53.85	34.01.69	23.47.12	6.55	SW	Os	5.39	0.65	SW, <5	E, <5	N/R	18.0
	34.03.50	23.53.85	34.02.44	23.46.06	5.82	SW	Os	7.03	0.96	SW, <5	E, <5	N/R	18.0
10/4/96	34.02.50	23.53.85	34.02.02	23.47.08	5.62	SW	Os	6.33	0.45	SW, <5	SW, 10	18.0	18.0
	34.03.50	23.53.85	34.02.87	23.48.69	5.50	SW	Os	4.93	0.60	SW, <5	SW, 10	17.5	18.0
10/14/96	34.02.42	23.53.63	34.02.89	23.55.39	4.25	NE	Os	2.17	0.58	SW, 15	SW, 12	17.1	17.0
10/15/96	34.02.36	23.53.76	34.01.86	23.54.67	4.53	NE	Os	1.05	0.58	W, 10	SE, 17	17	17.0
	34.03.48	23.53.00	34.02.76	23.54.97	4.63	NE	Os	2.23	0.82	W, 10	SE, 20	17	17.0
11/5/96	34.02.62	23.54.00	34.02.36	23.56.95	6.78	NE	Os	2.28	0.20	SW, 12	W, 12	18	18.0
	34.02.91	23.53.95	34.02.55	23.56.56	5.80	NE	Os	2.36	0.33	SW, 12	W, 12	18.5	18.0
	34.03.60	23.53.81	34.02.64	23.56.48	6.75	NE	Os	2.08	0.75	SW, 12	W, 12	18.5	19.0
	34.04.04	23.53.74	34.03.20	23.56.05	6.83	NE	Os	1.77	0.65	SW, 12	W, 12	18.5	17.0
11/6/96	34.02.55	23.53.75	34.03.83	23.51.80	5.72	SW	Of	1.79	1.18	SE, 15	SE, 25	18	18.0
	34.03.06	23.53.86	34.04.38	23.52.26	5.68	SW	Of	1.48	1.22	SE, 15	SE, 25	19	18.0
	34.03.60	23.53.72	34.05.08	23.52.14	5.90	SW	Of	1.41	1.32	SE, 15	SE, 25	19	18.0
	34.04.10	23.54.13	34.05.73	23.51.94	6.00	SW	Of	1.92	1.43	SE, 15	SE, 25	19	18.0
1/14/97	34.02.51	23.53.72	34.01.89	23.49.61	6.47	SW	Os	3.34	0.50	SW, 5	0	24	24.0
	34.03.54	23.53.88	34.03.07	23.49.72	6.43	SW	Os	3.39	0.38	SW, 5	0	23	24.0
1/15/97	34.02.48	23.53.81	34.01.33	23.43.48	9.03	SW	Os	6.00	0.67	0	SW, 5	23	24.0
	34.03.55	23.53.76	34.02.55	23.42.92	9.15	SW	Os	6.22	0.57	0	SW, 5	23	23.0
1/16/97	34.02.62	23.53.91	34.02.37	23.51.86	5.78	SW	Os	1.86	0.23	W, 12	W, 10	22	23.0
	34.02.08	23.53.82	34.02.54	23.50.43	5.92	SW	Of	3.01	0.41	W, 12	W, 10	22	22.0
	34.03.56	23.53.77	34.02.70	23.50.42	5.93	SW	Os	2.96	0.76	W, 12	W, 11	22	23.0
	34.04.05	23.53.89	34.02.88	23.50.54	6.00	SW	Os	2.93	1.02	W, 13	W, 12	22	22.5
1/17/97	34.02.62	23.53.98	34.02.61	24.00.58	8.83	NE	Os	3.92	0.01	W, 5	SE, 25	22.5	22.5
	34.03.08	23.53.97	34.02.98	23.59.80	8.30	NE	Os	3.69	0.06	W, 5	SE, 25	22.5	22.5
	34.03.61	23.54.10	34.03.22	23.57.58	7.60	NE	Os	2.40	0.27	W, 5	SE, 25	22.5	22.0
	34.04.07	23.53.78	34.04.22	23.56.36	7.05	NE	Of	1.92	0.11	W, 5	SE, 25	22.5	22.0

neutralised and moderate (16.5 to 18.4 cm/s) south-westerly currents had moved to these upper layers. Momentum in a westerly direction appeared to have increased at depth since 23h00 where the longshore drift in that direction registered between 14.2 and 17.0 cm/s. At 21h00 on day 2 (Figure 7.2a) the strong surface offshore currents had returned (up to 48.9 cm/s) and this trend was observed as deep as 58 metres where current velocity was a moderate 11.5 cm/s. Below this however, the deep longshore westerly currents that developed the previous night had spiralled slightly towards onshore and were measured between 12.1 and 13.4 cm/s. The pattern at 23h00 (Figure 7.2b) was similar to that observed at the same time the previous day where the offshore surface currents from 21h00 had swung to near south-westerly at 18 metres and westerly at 42 m. The spiral continued towards an onshore direction at 66 m where the current was recorded at a fast 32.6 cm/s. Moderate westerly currents near the surface at 01h00 (Figure 7.2c) spiralled onshore in the middle layers before turning back towards the west again at depth.

A strong south-westerly current of 38.2 cm/s near the surface was recorded at sunrise on day 1 during voyage #135 (Figure 7.3). Current velocity weakened through the middle layers as it spiralled towards the east, registering 10.1 cm/s at 66 m. Sub-surface westerly currents still dominated the pattern at midday on day 1 (Figure 7.3) as did the spiral to the east in the middle layers. At 60 metres, however, a 16.8 cm/s westerly current was recorded. Apart from the offshore component at 12 m on day 1 and the weak onshore currents at 20 and 28 m at midnight on the first day, all currents at sunset and midnight over both days (Figure 7.3) were flowing eastwards with no indication of a spiral below 20 metres. Currents were weakest in the middle layers, and stronger overall on day 2 with top speeds of 56.5 cm/s at 12 m and 55.6 at 60 metres. In terms of longshore drift the fastest recorded current was 60.4 cm/s and the slowest 1.1 cm/s. These translate into a potential maximum of 156.56 km and a minimum of 2.85 km covered in three days. The fastest current offshore of 47.1 cm/s works out to 122.08 km in 72 hours, while the minimum vector offshore of 1.4 cm/s translates into 3.63 km over three days.

It is evident that current direction and velocity can change rapidly both over time and depth and as a result, data from a single point source such as a moored current metre or a drogue which measures movement in only a specified layer of water, has limitations which must be taken into account.

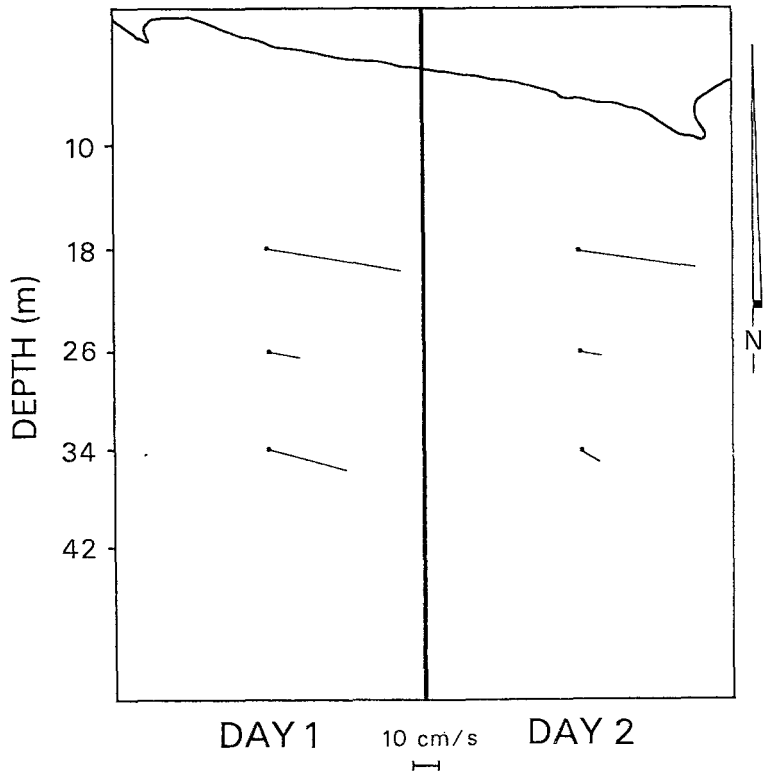


Figure 7.1 - ADCP vectors obtained at discrete depths inshore at Elands River just before sunset on the 7th & 8th October 1995 during voyage #131 of the R.S. *Africana*. The outline at the top of the figure is a trace of the coastline in the study area.

DISCUSSION

Apart from contributing to our understanding of reproduction patterns, isolated spawner-stocks, community stability, and energy flow (Norcross & Shaw 1984), oceanographic research has highlighted the importance of linking environmental trends with fluctuations in stock viability. In accordance with the member vagrant hypothesis (Sinclair 1988), the physical oceanography of a given region, in particular the currents, plays a crucial role in population regulation through enabling retention, and thus life cycle closure and continuity. Likewise, oceanography plays a significant role in determining the suitability of a habitat and the timing of spawning which is a key to completion of the larval phase under the banner of Iles & Sinclair's (1982) herring hypothesis. Even if one looks at the earlier critical period and match/mismatch hypotheses on population regulation (e.g. Hjort 1914; Cushing 1975, 1990a)

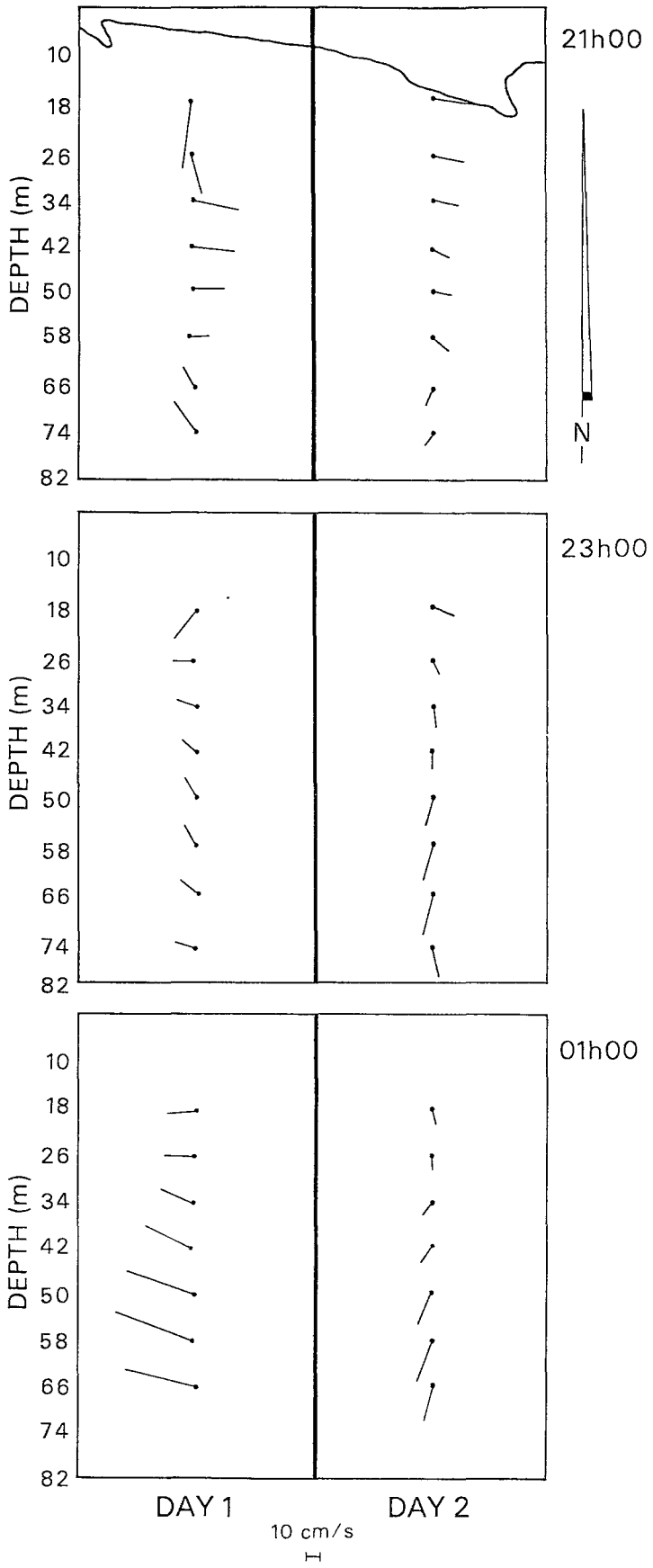


Figure 7.2 - ADCP vectors obtained at discrete depths offshore at Elands River at 21h00 (a), 23h00 (b) and 01h00 (c) on the 7th & 8th October 1995 during voyage #131 of the R.S. *Africana*. The outline at the top of the figure is a trace of the coastline in the study area.

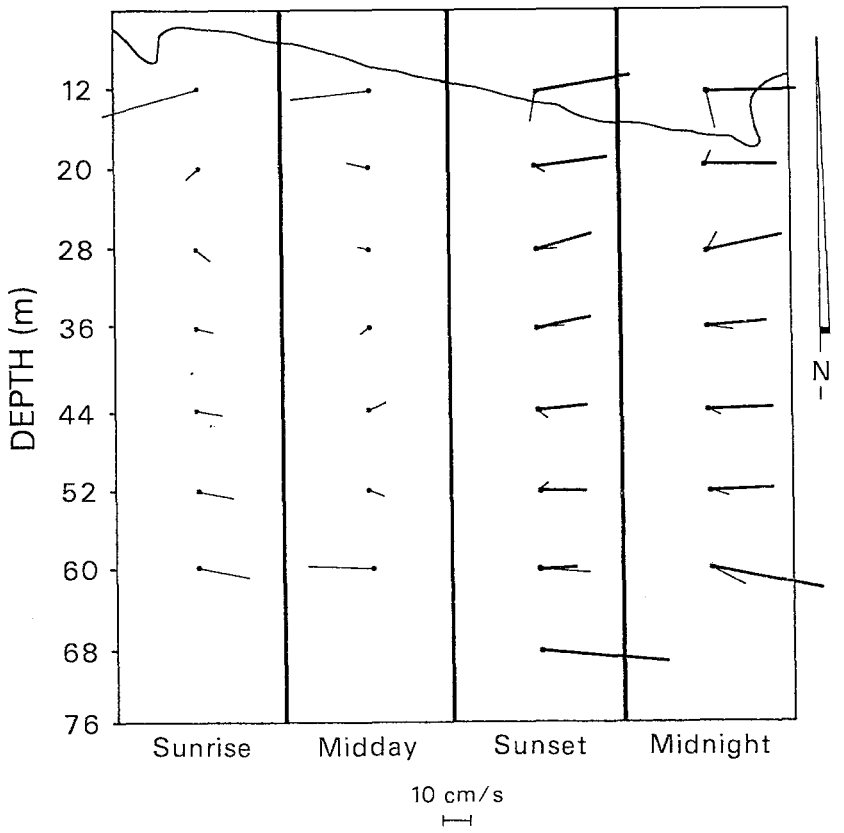


Figure 7.3 - ADCP vectors obtained at discrete depths off Bloukrans River at sunrise, midday sunset & midnight on April 25 and sunset & midnight on April 26 1995 during voyage #135 of the R.S. *Africana*. The vectors for the 26th April are represented by the broader lines. The outline at the top of the figure is a trace of the coastline in the study area.

the driving force behind seasonal phytoplankton blooms that provide the impetus for larval food production is correct physical conditions such as nutrient rich upwelling and homogeneous mixing of the water column.

The shelf-edge and continental slope are situated approximately 90 km offshore of the Storms River mouth (Tilney *et al.* 1996) and as such the thermal characteristics and circulation patterns in the neritic region close to shore will tend to be influenced by solar

radiation, forcing due to wind stress and tides rather than by dominant oceanic features (Schumann & Beekman 1984; Lutjeharms, Baird & Hunter 1986; Lutjeharms *et al.* 1996). The sub-surface cold water ridge which is present mainly during summer months over the central part of the eastern Agulhas Bank (Swart & Largier 1987; Hutchings 1992) exhibits a cyclonic circulation pattern (Hutchings 1994) with an easterly flowing component on the shoreward margin and a westerly flow on its oceanic side. This pattern of circulation together with eastward flowing counter currents emanating from the plumes breaking off from the inner margin of the Agulhas Current above the 200 m isobath (Lutjeharms *et al.* 1989; Boyd & Shillington 1994) may prevent loss of planktonic organisms to the Agulhas Current and help retain them in the neritic zone where chances of survival and recruitment are increased.

Many of the fishes found in Tsitsikamma are important components of either the commercial trawl- and line-fisheries or the recreational line- and spear-fisheries (Brouwer *et al.* 1997; Mann *et al.* 1997). Of these, the commercial component comprising offshore and pelagic species has the least to gain from MPA's such as the TNP that harbour spawner stocks of nearshore reef associated species. These reef species, comprised mainly of endemic sparids that are mostly stenotopic (Buxton & Allen 1989), are key components of recreational and commercial fisheries (Penney *et al.* 1989; Brouwer *et al. op. cit.*; Mann *et al. op. cit.*), where they are heavily exploited (Van der Elst & Adkin 1991). Sparids such as *C. laticeps* and *Petrus rupestris*, are known to be present in larger numbers within the TNP when compared to adjacent exploited areas (Buxton & Smale 1989). While *P. rupestris* is thought not to spawn in the TNP, but instead migrates either to the Transkei or offshore Agulhas Bank (Penney & Wilke 1993), *C. laticeps* does (Buxton 1987, 1990). This was confirmed by the presence of preflexion *C. laticeps* larvae in the waters of the TNP during the course of this project.

Based on the preliminary data obtained from the drogues and the longshore current components from the ADCP readings, it would appear that larvae may be dispersed considerable distances to the east or west of the TNP as well as onshore or offshore on a smaller scale. The mean longshore distance covered by a mass of water over a three day period extends to approximately 45 km past the east or western boundary of the TNP from the starting point off Storms River, while the maximum three-day longshore drift would

displace a water body approximately 146 km from either boundary. Larvae originating from closer to the boundaries of the park would therefore be prone to dispersal even further afield. The differences in current velocities and vectors with depth that were clearly evident from the ADCP patterns, however, means that dispersal could be restricted or controlled, or even avoided altogether through consistent larval behaviour patterns such as diurnal vertical migrations (Power 1986). The frequent longshore current reversals also mean that nett displacement may be minimal if larvae remained within the same body of water.

While recently hatched larvae of most marine fish species are capable of only minimal directed movement (Lyne & Thresher 1994), most late stage larvae and even some small larvae are capable of controlling their position in the water column through active swimming, buoyancy control and reaction to physical properties (Richards & Lindeman 1987). Observations on swimming speed in pre-settlement and late pelagic larvae of coral reef fishes (Leis, Sweatman & Reader 1996; Leis & Carson-Ewart 1997) revealed average speeds ranging from almost zero to 20 - 30 $cm.s^{-1}$, while a single *Myripristis* species was recorded at 65.5 $cm.s^{-1}$. These measurements for larvae which ranged in size from 7.0 to 55 mm BL, translate to an average swimming speed of around 13.8 $BL.s^{-1}$, with some of the faster species attaining 40 $BL.s^{-1}$. Chaetodons, acanthurids, lutjanids, blenniies, holocentrids and some pomacentrids (*Chromis atripectoralis* and *Neopomacentrus azysron*) exhibited faster speeds than apogonids, ephippidids and the *Pomacentrus* species. The speeds detected by Leis & Carson-Ewart (*op. cit.*) for coral reef fish larvae were far superior to those recorded for temperate fish larvae (Blaxter 1986 in Leis & Carson-Ewart *op. cit.*), which may have implications on the degree to which larvae from the temperate south-east coast of South Africa can behaviorally influence their movements.

Several studies by Stobutzki & Bellwood (1994, 1997) provided information on the sustained swimming abilities in coral reef fish larvae. Using a chamber to simulate currents of varying speeds, Stobutzki & Bellwood (1994) observed that most larvae used their pectoral fins for slow speeds and caudal fin and body undulations at higher speeds. In several species (Dischistodus spp. and Pomacentrus amboinensis) pre-settlement larvae were better swimmers than post-settlement juveniles, with speeds of between 8 and 56 $TL.s^{-1}$ being maintained for close to an hour. Analysis at the family level (Stobutzki & Bellwood 1997) showed that the Acanthuridae were the most durable, maintaining the controlled speed of 13.5 $cm.s^{-1}$ for 194.3

± 15.5 hrs and covering an effective distance of 94.4 ± 7.5 km. Nemipterids were least capable of maintaining great speeds, covering on average only 3.6 ± 2.5 km over 7.4 ± 4.8 hrs at 15 $cm.s^{-1}$. Larger fish larvae tended to swim for longer periods, presumably because speed was relatively slower (3-4 $TL.s^{-1}$ for large acanthurid larvae as opposed to 10 $TL.s^{-1}$ for smaller fish. In addition, larger larvae have larger metabolic reserves and slower metabolic rates

The larvae studied by Leis *et al.* (1996), appeared to be able to control their position in the water column and could detect reef/settlement areas up to one kilometer away. Whether these swimming capabilities are present throughout the larval phase or only in pre-settlement fish is unclear. Nevertheless, this means that nett displacement may well be more reliant on behavioural patterns of the larvae during the middle to late developmental stages than on passive drift (Harden-Jones 1968) and current directions and speed, with late pelagic larvae being able to actively enhance or retard their dispersal (Leis & Carson-Ewart 1997). The sustained swimming abilities demonstrated by Stobutzki & Bellwood (1994, 1997) also demonstrated the potential for larvae to control dispersal and settlement patterns, and hence ultimately community structure. Information such as this highlights the possibility of self seeding of reefs distant from spawning grounds in the absence of favorable oceanographic features (currents & gyres) by active and sustained swimming. A further implication of their work could provide explanations for net avoidance behavior and the ability of larvae to swim towards passive sampling systems such as light traps. The retention of *Clupea harengus* in the western Atlantic (Stobo *et al.* 1973; Bradford & Iles 1993) as opposed to their widespread dispersal in the north-east Atlantic (Clark 1933) reflects the importance of local oceanographic conditions over behaviour in some species.

Large-scale offshore displacement of plankton would presumably occur when the dominant thermohaline process of upwelling takes place at major headlands along the Cape south coast (Schumann *et al.* 1982, 1988; Boyd & Shillington 1994) during spring and summer causing mass offshore movement of neritic waters. Poor catches of fish larvae under upwelled conditions in the TNP (Tilney & Buxton 1994) were taken as an indication that they had been displaced offshore. The survivability of larvae during upwelling is, however, questionable if they do not remain within the displaced warm water, as sudden temperature drops are more conducive to retarded development and large scale mortality of fish in the TNP (Hanekom *et al.* 1989). The longshore jet-current that is set up at the warm/cold water

interface (Schumann *et al. op. cit.*) operates in a south-westerly direction. Upwelled water may therefore be displaced as much as 75 km offshore and 200 - 250 km longshore during an upwelling event lasting between ten and twelve days (Schumann *et al. op. cit.*). Larvae that are displaced this far have the potential to settle in nearshore regions far to the west of their origin in the TNP when the upwelled waters they occupy move back onshore as part of the inshore current-closure system (Tilney *et al.* 1996) as the upwelling event nears its conclusion.

Data obtained from a "Neil Brown" ACM2 acoustic phase-shift current meter moored at a depth of 48 metres on Middlebank between July 4 1991 and January 17 1992 (Tilney *et al.* 1996) also reflected a dominant longshore current component driven by CTW's that were induced by eastward moving synoptic features (Schumann & Brink 1990) with a periodicity of two to four days and speeds up to 17 cm/s. This longshore current oscillation was found to occur all year round, but was most dominant during winter. The tidally influenced cross-shelf currents were only a minor component with onshore and offshore speeds of 0.2 and 0.1 cm/s respectively (Tilney *et al. op. cit.*). These authors also quoted a maximum value of 19 cm/s longshore obtained from a current meter deployed at 25 metres in March and April 1991 (Eckhart Schumann, Department of Oceanography, University of Port Elizabeth, Unpublished Data). These values are considerably lower than the maxima obtained from the drogue traces and the ADCP near-surface vectors in this study. The possible reason for this, given by Tilney *et al.* (*op. cit.*) is that surface waters are under a greater influence from wind stress (Schumann 1987) such that stress operating in the same direction as the surface current will greatly enhance velocity. Nevertheless, assuming that sparid larvae were passive drifters, Tilney *et al.* (*op. cit.*) concluded that the potential for their dispersal beyond the TNP boundaries existed, with the greatest potential existing during the spring/summer upwelling season when many of the linefish species spawn (Buxton 1990; Buxton & Clarke 1989, 1991; Mann 1992; Steve Brouwer, DIFS, Rhodes University, Unpublished Data). Permanent loss of nearshore larvae to oceanic waters appears unlikely, as the region is dominated by current closure systems that serve to retain ichthyoplankton within neritic waters. The current patterns described during this study were in agreement with the findings of Tilney *et al.* (*op. cit.*) and also served to enhance our knowledge with the addition of the complete vertical current profile pattern.

While nursery or settlement areas for reef and sand associated fish are plentiful within the nearshore zone of the TNP, similar habitats are available along most of the south-east coast (Tilney *et al.* 1996). So although larvae may remain close to the site of spawning due to the availability of suitable settlement grounds, widespread dispersal beyond the boundaries of the TNP may still provide the larvae with a better than reasonable chance of encountering similar environments (see Colin 1995). Even if larvae are transported to areas not suitable for settlement, they may enter a reduced growth or competent phase which delays metamorphosis, thereby increasing the chances of finding appropriate settling grounds. Such behaviour has been noted for larvae of the marine gastropod *Cymatium parthenopeum* (Pechenik, Scheltema & Eyster 1984), the wrasses *Thalassoma bifasciatum* (Victor 1986) and *Semicossyphus pulcher* (Cowen 1991), and King George whiting *Sillaginodes punctata* (Jenkins & May 1994). However, the inability of larvae to find a suitable settlement reef in time can be responsible for fluctuations in recruitment (Gabric & Parslow 1994), and some workers believe that this is greatly influenced by larval patchiness (Victor 1986; Doherty 1988) where concentrated larval densities which pass over reefs at the right time are reflected in observed recruitment pulses.

In terms of the TNP seeding adjacent exploited areas with the early life history stages of fishes, one must assume that larvae remain within the same body of water whose movement was represented by the drogues. However, endogenous and external factors can initiate behavioural mechanisms which could potentially modify passive transport by currents (Koutsikopoulos, Fortier & Gagné 1991), either retarding or enhancing horizontal displacement (Champalbert & Koutsikopoulos 1995), as was emphasized by Leis & Carson-Ewart (1997) and Stobutzki & Bellwood (194). The potential for retention or dispersal through vertical migrations to utilise current reversals or currents of different strengths must be considered (see Miller 1988), and although no clear patterns of diurnal migrations were evident from the discrete depth work (see Chapter 6), samples were few and larval concentrations generally on the low side. Tilney *et al.* (1996) also found that sparid larvae were homogeneously distributed leading them to conclude that they did not exercise preferred position retention and were prone to dispersal by currents. However, if there is retention amongst any of the larvae it may be taking place on a larger scale than in the vicinity of the spawning site, i.e. in an area of several nautical miles instead of metres. For example, larvae

sampled at the sites five nm offshore along the transect (see Chapter 5) may have originated from reefs within the TNP and may be part of a circulation pattern which could return them there. The chances of this being the case for those larvae from reef-associated species at 10 and 15 nm are less but not impossible given the scale of some oceanographic features. The absence of any significant differences between larval concentrations from the different transect sites must be interpreted carefully. If the study area or transect had been extended out to the shelf-break (90 km offshore) instead of just 15 nm and the distance between stations had been greater there may well have been trends. Larval patchiness must always be considered when attempting to discern distributional patterns, and trends in horizontal distribution may well be obscured due to intense tidal regimes and tidal currents (Tanaka 1985) which displace larvae in a horizontal direction on a daily basis. In addition, the absence of any apparent inshore retention within the study area may well be a true reflection of the species concerned. No sampling took place in the surf zone or intertidal area which has been shown to harbour species which resist offshore and even longshore dispersal (see Marliave 1986) perhaps by using visual landmark cues, velocity (current) gradients (Shaw & Tucker 1965) and surf zone circulation cells (McLachlan 1990a, b). It has been proposed that the larvae, like the adults of some intertidal fish, have a narrow tolerance of substrate types which they would use for settlement (Marliave 1977). A strong affinity for the correct substrate types would therefore favour the evolution of retention strategies which would ensure this.

Nevertheless, the apparent lack of retention for most species (including sparids from the point of view of the TNP) is encouraging from the dispersal potential point of view as fast moving longshore currents that dominate the pattern could move larvae to adjacent exploited areas. While it is realised that the potential for widespread dispersal from the TNP exists, much still depends on the adult mode of spawning, and behaviour of the larvae themselves. Not only does more work need to be done to discern vertical distributional patterns in relation to currents, as small differences in vertical placement can result in large variation in horizontal transport (Power 1984; Miller 1988), but a more detailed series of ADCP readings is needed in concert with more intensive drogue work in order to fully unravel the oceanographic dynamics within the TNP.

In an article written by Warren Wooster (1988), it was stated that, "Important scientific problems often lie in the zones where disciplines overlap, and thus require interdisciplinary collaboration. Although there are urgent problems that require the joint efforts of oceanographers, meteorologists, and fisheries scientists, such collaboration has proved difficult to arrange." A similar sentiment was echoed by Sammarco (1994) who declared that an individual approach will only retard our attempts to understand complex processes, and that a multi-team approach which is truly interdisciplinary in nature would be the more effective option. Fortunately, in recent years there has been a good working relationship between investigators from these various fields in the TNP, and the prospects for continued collaboration are encouraging. Information that can be gathered from interactive endeavours such as this, is fundamental to the understanding of the effectiveness of MPA's and could ultimately be incorporated into determining the effective sizes and frequency of reserves along the coast such that maximum protection is afforded the spawner stock while at the same time maximum benefit is derived by neighbouring fisheries.

CHAPTER 8 - FINAL DISCUSSION

Ichthyoplankton Research in Southern Africa

International recognition of ichthyoplankton research in southern Africa was a slow process. The first publication on early life history stages of fishes has been attributed to the Norwegian, G. O. Sars, who described the development of cod eggs and larvae in 1879 (Ahlstrom & Moser 1981). Subsequent to this, early pioneers in the field published extensively on the pelagic phases of many important commercial species between 1879 and the turn of the century. In an overview of the history and status of systematics and development of early life history stages in fish Ahlstrom & Moser (*op. cit.*) single out researchers from England, Italy, the United States and Germany. They also include Johan Hjort from Norway whose work at the turn of the century fuelled the eventual development of his controversial "critical period" hypothesis (Hjort 1914). Milestones in ichthyoplankton research during the first decade of the 1900s are attributed to workers such as C.G.J. Petersen and J. Schmidt from Denmark and E. Ehrenbaum from Germany. Nowhere is there mention of the early work of John Gilchrist who was the first to collect and describe the pelagic propagules of fish from the Cape of Good Hope during this early period.

Since the latter half of the 1970's however, exposure outside of peer reviewed journals of South African research in this field has been achieved through presentations at international conferences or symposia. Aspects of southern African ichthyoplankton which have been presented included larval fish assemblages and ocean boundaries, estimations of fish biomass through ichthyoplankton surveys, fish larval systematics and descriptions. A selection of some presentations are described below. Shelton & Hutchings (1981) delivered a paper on the influence of the Benguela environment on sapwning and recruitment in *E. japonicus* at The Early Life History of Fish: Recent Studies conference at Woods Hole, California in 1979. The paper on ichthyoplankton interchange in the mouth region of the Swartkops estauary presented in Southampton by Alan Whitfield in 1988 was later published in a internationally recognized journal (Whitfield 1989a). The larval fish assemblage in the Benguela system on the west coast was dealt with by Olivar & Shelton (1993), while daily egg production by *E. japonicus* in the same system was discussed in terms of population assessment and management (Shelton, Armstrong & Roel 1993). Harris (1993) dealt with the Kosi estuary ichthyoplankton community at the Pre-Indo-Pacific Fish Conference workshop in Indonesia, and the larvae of the St Lucia estuary were dealt with at the 4th Indo-

Pacific Fish Conference in Bangkok (Harris & Cyrus 1995b). During the same conference, Beckley (1993b) presented data on the larval fish assemblages in relation to oceanographic features in the Agulhas Current. The Kosi estuary larval assemblage was again the topic of a paper by Harris (1994) at the 18th International Larval Fish Conference in Canada. A few years later Beckley & Connell (1996) and Harris & Cyrus (1996) presented papers at the international conference in Sydney on bluefish (*Pomatomus saltatrix*) larvae and surf zone larval assemblages respectively. Both Lynnath Beckley and Carl van der Lingen co-authored separate papers at this conference in Sydney on *Lampanyctus* species found in the Agulhas Current (Olivar & Beckley 1997) and the larval development of the galjoen, *Dichistius capensis* (Leis & van der Lingen 1997).

The data gathered during the course of this study made a significant contribution to the data base on the coastal and neritic ichthyoplankton community and its seasonal dynamics along the south-east coast. In addition, this survey also provided new information on species whose distributional ranges have previously only been defined from adult and juvenile records (see also Sharp 1981). The absence of high concentrations of larvae during months when cool upwelled waters were present during this study points to an adverse effect on survival. Eggs were still present in high concentrations during these periods leading to the hypothesis that fish were spawning irrespective of the upwelling condition in the hope that larvae would find suitable conditions in which to survive. Once hatched, however, mortality is high (Tilney & Buxton 1994) unless cells of warm water can be found, and this presumably led to the low catches of larvae at these times. A similar observation was made by Tilney & Buxton (*op. cit.*) when they found low larval concentrations at times of upwelling in February and March of 1992.

The fact that the majority of species sampled during the preliminary vertical distribution study appeared to be evenly distributed throughout the water column at various stages of development had encouraging implications for the sampling strategy employed for most of the study period. Sampling with bongo nets to a maximum depth of 18.5 metres in this study meant that while estimates of abundance and hence mortality could not be calculated due to the likelihood of larvae occupying the space below the sampled depth, the probability that a good representation of the species assemblage was obtained is high (see Brodeur & Rugen 1994). The prolonged sample period over three years also increased the chances of encountering specimens from most species in this surface layer. There were no larval species encountered in the deep layers during the RMT work that were not caught in the upper 18.5 metres at another stage during the program. Due to

the possibility of active retention in the intertidal or surf zone by intertidal species (Marliave 1986), it is probable that the only larvae not sufficiently represented during this study would have been those restricted to this zone, as sampling that close to shore along the Tsitsikamma National Park (TNP) coastline is not an option due to severe wave action and shallow reefs.

Hollowed (1992) issued a word of warning considering observed distributional patterns in *M. productus*, although it is applicable to ichthyoplankton in general. She stated that the distribution of (*M. productus*) larvae exhibit both temporal and spatial patchiness and as such sampling at a few selected sites each month cannot provide an accurate reflection of birth and mortality rates. Likewise, the true picture of temporal and spatial distribution of the ichthyoplankton assemblage within the area covered by this study may only be revealed once more intensive sampling (greater frequency and more sites) has been performed.

The Ichthyofaunal Species Assemblage of the TNP

In previous studies on the distributional patterns of the littoral ichthyofauna of the TNP, Buxton & Smale (1984) recorded 65 species from 29 families, while Burger (1990) identified 116 species from 46 families using visual census techniques and rotenone collections. These included 12 species of sharks, three rays and the lesser guitarfish, *Rhinobatos annulatus*. The latter study also drew from the checklist compiled in the former work but missed out several species, e.g. the humpback toadfish *Chatrabus melanurus*, bigeye clingfish *Diplecogaster megalops* and African gurnard *Trigloporus lastoviza africanus*. Certain of the species identified from plankton tows during this study and in the previous study (Tilney & Buxton 1994) are not reflected in the checklist for the area, and illustrates that although adults of some species have only been recorded or observed outside of the boundaries of the reserve, their larvae enjoy the relatively pristine conditions provided within. Unspoilt reef and softer sediments undamaged by trawling may well provide greater opportunities for settlement after which sub-adults migrate to join the main stocks. Another plausible reason for their exclusion would be that their habitat comprising deeper offshore waters would not have been sampled by the conventional means used in these studies. For example, adult snoek (*T. atun*)are regularly caught at the snoek banks, situated at 34° 14' 00" S, 24° 05' 04" E to the east of the park, but have never been recorded in the reserve. Their larvae were, however, sampled within the park's boundaries during this study. If a complete checklist of the ichthyofauna in the TNP is to be established, specimens from all stages of the life history of

those species concerned would have to be included. Combining the surveys of Buxton & Smale (*op. cit.*), Burger (*op. cit*), Tilney & Buxton (*op. cit.*) and this study, and including fish caught during the ongoing offshore and shore-tagging projects, an updated checklist for the TNP (Appendix 16) has been produced. Fish whose distribution is said to include the south-east coast in general (Smith & Smith 1966; Smith & Heemstra 1986) are not included if they do not appear in any of the aforementioned surveys or if they have not been observed during any of the ongoing tagging programs, as it is not stated whether or not the fish were sampled from within the boundaries of the TNP. Certain personal observations (Aidan Wood and Steve Brouwer, DIFS, Rhodes University) made while diving in the TNP are also included.

According to island biogeography theory, species diversity is a function of island size and proximity to similar habitats (Preston 1962) and is maintained at an equilibrium determined by rates of extinction and immigration (MacArthur and Wilson 1967). In applying the equilibrium theory to conservation biology it was originally thought that a large nature reserve would mean greater diversity than a number of smaller ones (Diamond 1975). The more modern trend, however, is the belief that number of habitats determines diversity such that several small reserves incorporating many habitat ranges would support more species than a single large reserve whose area comprises fewer and similar habitat types. The TNP is one of the largest Marine Protected Area (MPA) in southern Africa. Collated data used to construct the species checklist (Appendix 16), showed there to be 171 species of fish from 70 families which have been positively identified within its boundaries. Without a direct comparison with several smaller areas it is difficult to make a judgement on the reserve size/diversity debate, although the position of the reserve in the temperate/sub-tropical transitional zone and its composite habitat types seem to side with the single large reserve producing maximum diversity argument. As Bond (1989) states, the importance of a region should not be judged in terms of the number of species it contains but in the quality and importance of what it contains. The TNP contains abundant spawning populations of the main component species of the linefishery and as such should be considered important. Many of the MPA's worldwide are considered too small to be protected against outside influences (McAllister 1995) and it is recognised that island biogeography theory studies should be incorporated when determining reserve sizes in different ecosystems. In determining the optimum size for a place such as the TNP, larval distribution, length of planktonic phase, and local current patterns must be used in combination so that reserve size becomes based upon distances from fishing grounds which

could conceivably be covered by dispersing ichthyoplankton. In terms of conserving biodiversity, all species should be considered, but this leads to a dilemma. The majority of the fish species connected to the linefishery are endemic, and are sedentary and highly territorial as adults, but they have pelagic egg and larval phases which are prone to dispersal. Other species such as gobiids which have demersal eggs and clinids which are viviparous do not have great dispersal potential. It is therefore a matter of priorities. If the first priority of the TNP is to bolster the linefishery, then reserve size should be determined based upon the life history of the species concerned, i.e large enough to support viable spawner stocks yet small enough for dispersal of young to exploited areas. Care must, however, be taken not to assume too much as dispersal of planktonic larvae may not take place over any great distances (Hockey & Buxton 1989) due to macro- and mesospatial distributions.

Looking at the three levels of diversity (Cody 1975) one is faced with alpha diversity which is defined as the number of species within each habitat within a specific region such as a nature reserve; beta diversity which measures the number of these habitats and the interchange between them within the same region; and gamma diversity which describes the crossover of species between like habitats in separate geographic regions. In the context of the TNP, alpha diversity would measure the species number at a particular reef site such as Middlebank. Beta diversity would incorporate all reef sites and the interchange of adults, juveniles and planktonic stages within the reserve boundaries, while gamma diversity would be a measure of the movement or turnover of fish species from a reef habitat within the reserve to one outside, e.g. Middlebank to Grootbank off the Salt River west of Natures Valley. In a further move Cody (1986) used these terms to describe the status of rare species and defined beta rarities as species which were habitat specialists. The highly resident and sedentary life history styles of many of our reef fishes would class them as habitat specialists, and the best way to conserve these species (Bond 1989) would be to set aside an area with the required habitat and prevent its degradation. This is one of the functions of the TNP when it comes to conserving our important linefish species. The importance of seeding areas adjacent to the TNP through the export of fish eggs and larvae is seen as a probable function of the TNP, and one that needs to be assessed and quantified as a matter of priority. During the course of this project, the need for a detailed study of the dispersal dynamics of eggs and larvae of reef associated fish species from the TNP was recognised. The preliminary stages of this endeavour have been completed and were discussed in Chapter seven.

Marine Protected Areas, Ichthyoplankton, and the Future

"Roll on, thou deep and dark blue ocean - roll!
Man marks the earth with ruin - his control
Stops with the shore."

This sentiment penned by Lord Byron almost 200 years ago may have seemed plausible then, but is only laughable now. The control has extended far beyond what he could have imagined. A control for the worse, driven by financial greed and the requirements of a population whose numbers this planet was never meant to support. More recently, another form of control is being exercised, that which restricts man's destructive activities in an attempt to turn the tables on the degradation of marine life. One of the more modern aspects of this control, and one which is gaining in both momentum and support worldwide is the establishment of MPA's to ensure that future generations will be able to appreciate the world's greatest wonder - the bounty of the ocean.

"In 1993, 69% of the world's marine stocks were fully to heavily exploited, over exploited, depleted or slowly recovering from overfishing." (FAO 1995). Despite this only 13% or 1 270 out of 9 832 protected sites around the world are in the sea (WCMC/IUCN 1993) covering 0.25% of the ocean's area over the continental shelf. Now in 1997 the situation is even worse despite greater efforts and greater awareness. It is time for extreme measures and to act boldly. MPA's have been in existence for a number of years in southern Africa and it has only been recently that they have been viewed as the only truly viable option for the future of linefish conservation (Bennett & Attwood 1993; DeMartini 1993; Attwood, Beaumont, Branch, Densham, Dye, Feely, Harris, Heydorn, Hockey, Hutchings, Mann, Penney, Taylor, Williams & Yssel 1997). Traditional methods aimed at regulating catch or fishing effort in the form of multispecies daily bag limits (Attwood & Bennett 1995), size limits and seasonal closures are difficult to implement due to lack of education and enforcement. Marine Protected Areas (MPA's) on the other hand offer a safe haven for fish species and recently this form of protective management has been viewed as an enforceable and cost-effective alternative (see DeMartini 1993; Attwood *et al.* 1997) while providing the perfect venue for recreational and educational practices. Essentially, habitats are protected from human induced damage resulting from fishing and other recreational activities such as diving, thereby making safe refuges available to exploited linefish species and those with

specialised habitat requirements (Roberts & Polunin 1993b). Additional advantages of MPA's have been listed as being able to enhance nearby fisheries through new recruits and emigration, reduce the need for the collection of biological data for fished species, protection and conservation of genetic diversity, and maintaining natural populations and community structures (Bohnsack 1990; Roberts & Polunin 1991, 1993a; Attwood *et al. op. cit.*). However, many MPA's are subject to poaching and other external influences such as development and industry and their associated pollution (McAllister 1995). Solutions to these problems must be found and implemented soon before the cascade towards total extinction becomes irreversible. Whereas in the past MPA's were seen primarily as areas which could protect certain individual species from exploitation, they are now acknowledged as having a more diverse function in protecting marine ecosystems as a whole (King 1995) and preserving biodiversity.

Preserving biodiversity within the boundaries of an MPA may not be enough reason to justify its existence. Instead the benefits it has for local and surrounding communities and industries may become the measure of success. As stressed by King (1995) one of the considerations which must be taken into account when proposing MPA's is positioning them so that local oceanographic conditions will result in seeding adjacent exploited areas through the drift of pelagic ichthyoplankton. Although enhancement of neighbouring fisheries may come directly from settling postlarvae which have been transported from within protected boundaries, the resident adult populations within MPA's are vitally important. Large adult populations in reserves should be seen as spawner stocks (Roberts & Polunin 1993a), the larger and more intact they are, with large individuals, the greater the egg production will be.

The virtual lack of specific studies aimed at the role that marine reserves play in the early stages of fish ontogeny, especially in terms of their retention or dispersal and the implications of this for fisheries, is disturbing. The need for this both internationally and in the South African context has been recognised for many years (Hockey & Buxton 1989; Roberts & Polunin 1991) and appears to have been reiterated *ad nauseum* in subsequent years (Buxton 1993; Carr & Reed 1993; DeMartini 1993; Dugan & Davis 1993; Roberts & Polunin 1993a, b; Attwood & Bennett 1994) but very little has been done about it. For example, recent studies on the dusky grouper, *Epinephelus marginatus*, in the Medes Islands Marine Reserve (Zabala, Garcia-Rubies, Louisy & Sala 1997; Zabala, Louisy, Garcia-Rubies & Gracia 1997) have stressed that almost all aspects of early

planktonic life in this species are unknown and that this gap needs to be filled to ascertain dispersion and colonisation patterns which would aid in their sustainable management. A preliminary survey of the ichthyoplankton has been performed in the TNP (Tilney & Buxton 1994; Tilney *et al.* 1996) which acted as the springboard for this study. These studies concentrated on basic distributional patterns and inferred retention from adult spawning habits and the types of substrates larvae were captured over. Potential for dispersal based on length of the pelagic phase and on current patterns obtained from a short term data series from a single fixed point current meter was briefly discussed.

A common belief is that the high densities of reef fish present in MPA's means that the excess numbers will overspill and enhance adjacent populations (Roberts & Polunin 1993a), resulting in increases in catch per unit effort (CPUE) for a particular species, e.g. *Dichistius capensis* and areas adjacent to the De Hoop marine reserve (Bennett, Attwood & Mantel 1994). Although there have been a few recorded cases where exploited areas have benefited from an MPA (Cole *et al.* 1990; Bennett & Attwood 1991) through the migration of adult fish such as *D. capensis* (Attwood & Bennett 1994), the larger picture incorporating early life history stages has been sorely neglected. The fact that the majority of the target fish in the South African line- and spear-fishery are highly resident reef species augments the need for an in-depth probe into the potential for recruitment through ichthyoplankton dispersal. Many marine creatures, both vertebrate and invertebrate, have planktonic early life history stages (Roberts & Polunin 1993a). These eggs and larvae which are spawned in open seas may travel vast distances in oceanic currents before metamorphosing and settling back onto the reef habitat.

Studies on the dispersal patterns of teleost fish eggs and larvae are well represented in the literature. However, the virtual lack of research into the role that MPA's play in the early life history of fishes, especially in terms of their retention or dispersal and the implications of this on the management of fisheries, is disturbing. The overall objective of the research work which has been undertaken in the TNP since 1980 is to investigate the role of MPA's in the conservation of coastal fishes. The TNP has been shown to be an effective conservation option for the resident populations of adult and sub-adult reef fish. However, an understanding of the role that marine reserves play in the seeding of adjacent areas is lacking on a worldwide basis (Roberts & Polunin 1991), and although it is known that most coastal marine fish spawn buoyant eggs, there is a lack of

knowledge as regards the flux of these eggs and larvae originating from coastal zones (Lobel & Robinson 1986). Apart from this study and the earlier surveys by Tilney & Buxton (1994) and Tilney *et al.* (1996) there has been no other published work concerning ichthyoplankton and MPA's.

Significantly higher numbers of sub-adults and adults of two out of three studied reef species (*C. laticeps* and *P. rupestris*) were recorded in the TNP when compared to a heavily exploited area (Cape Recife) approximately 150 km to the east (Buxton & Smale 1989). The third species, *C. cristiceps*, was also more abundant but not significantly so, although it was recognised that its numbers could have been underestimated from visual transects due to its shy nature. It is clear therefore that adult populations of certain species have derived benefit from the protection afforded by the TNP, but until it can be ascertained where eggs and larvae are originating from care should be taken with interpretation. As part of the future work in the area, it is anticipated that regular samples will be taken from areas adjacent to the TNP. Comparisons will be made with respect to species composition and abundance in an attempt to quantify the effect of the TNP on spawner stock size, spawning success, and larval survival. Whether the larvae of these sparids, or any of the species, are actually protected while in the reserve to the same extent as the adults is debatable. While larvae are not subjected to fishing mortality either within or outside the TNP, levels of natural mortality have not been quantified. It is arguable that because conditions are closer to pristine in the TNP, that predator concentrations and hence natural mortality would also be higher. While a larger spawner stock may produce more propagules to counter the effect of predation, the net survival rate of early life history stages may be the same as in an exploited area. The important consideration is the fate of the surviving eggs and larvae. Are they retained within the boundaries of the TNP where they settle and further enhance the abundant populations or do they get dispersed to bolster threatened populations in exploited areas? Seven of the sparid species caught in this study could not be identified past family level. While this is not seen as ideal, it is recognised that in the context of the entire TNP program it is vital that the dynamics of sparid larvae be investigated. For this to happen all types present in the plankton need to be identified, and future work will concentrate on this group. It is anticipated that the status of our knowledge on the eggs and larvae of the sparids will greatly improve once all our efforts are concentrated towards them.

In order to concentrate on the sparid fishes in the near future, a sampling strategy based upon the preliminary results from this study will be initiated. The positioning of sparid larvae in the water column remains unclear. Catches during the vertical distribution study were poor, with only *B. immornata* and Sparidae Species 6 featuring in voyage #131 catches and Sparidae Species 10 in voyage #135 catches. The chances of obtaining dedicated ship time for more discrete depth work are poor, and so the new program will have to be designed around the assumption that vertical distribution is equal. Although concentrations of sparids in this work were low, it is in agreement with the findings of Tilney *et al.* (1996) who also declared that this group were evenly distributed over all substrate types and along an offshore transect. In this study they appeared to be homogeneously distributed offshore to 15 nm even though sampling at this site was terminated at an early stage. It is, however, encouraging to note that larvae of most linefish were found to be scarce or absent in stations up to 100 km offshore sampled by Beckley (1993a). The stations at Middlebank and five and ten nautical miles all produced sparid larvae on a frequent basis, with *A. argyrozona*, *C. laticeps*, *D. s. capensis*, *P. b. natalensis* and Sparidae Species 11 being most abundant. The paucity of sparid larvae in night-time catches may have been an indication of extreme diffuse distribution and patchiness, or net avoidance. Very few species showed any sign of seasonality, with only *A. argyrozona*, *P. b. natalensis* (both winter), *D. s. capensis* (winter and spring), and *S. emarginatum* (spring) exhibiting any significant seasonal differences. Overall it appeared that August/September and November were productive times for catching sparid larvae, although infrequent sampling in December and January may have obscured the true picture.

The galjoen, *Dichistius capensis*, is an abundant species from the inshore surf zone (Attwood & Bennett 1994) and comprises one of the major components of the rock and surf tagging program in the TNP. It was considered unusual that over the three year sampling period, no larvae were captured. A similar sentiment was echoed by Tilney & Buxton (1994) during the first TNP ichthyoplankton survey. In their description of laboratory reared *D. capensis* larvae, Leis & van der Lingen (1997) also refer to the paucity of wild caught larvae. It is assumed that spawning takes place inshore and that there is active retention of the early life history stages in the surf zone. In addition to the concentrated effort required for the Sparidae, the capture of these larvae in the field, perhaps with the aid of light traps, should be

viewed as a priority as it may well shed some light on the dynamics involved with the retention process.

In order to counter the early dispersal of egg and larval stages and reduce the influence of patchiness, sampling with actively towed bongos will have to be conducted more frequently, especially during the months which have been identified as being highly productive. A concerted effort will also have to be made to sample over the December/January period, a time which is well documented in the literature as being the peak spawning period for many sparid species. In order to facilitate a more intensive sampling program, only stations inshore will be sampled, with most of the effort being concentrated over the reef-rich areas as close to the surf zone as possible. Although an intense night sampling strategy may lead to higher sparid catches, the danger of working at sea at night off this coastline would most likely preclude this option. The alternative which is being considered is the use of aggregating devices such as light traps. Unlike towed gear which relies on speed and flow patterns to capture larvae, they are operated passively with the knowledge that fish larvae can be attracted to light (Leis & Rennis 1983; Doherty 1987) and from there into a trap (Choat *et al.* 1993). Apart from being able to sample throughout the night, light traps can be used during periods of high productivity when algal blooms preclude the use of active samplers because of excessive clogging (Gregory & Powles 1988). The catches from these traps will be used to augment data gathered by the bongos which are efficient for quantitative collection but fall short when it comes to accurate representation of size distributions, and being able to sample physically obstructed, shallow regions (Gregory & Powles *op. cit.*) such as the nearshore zone in the TNP. Light traps will either be used on their own or will be attached to satellite tracked drogues left out overnight. The distance covered overnight with the drogue, together with the role the light plays in attracting larvae should reduce the effect of patchiness on catches substantially. In addition, light traps are known to catch larger specimens (Choat *et al. op. cit.*) which would normally evade towed gear such as bongos. Most larvae tend to become more responsive to light intensity as ontogeny progresses, making the larger sizes more susceptible to the gear (Gregory & Powles *op. cit.*). This alone could have far reaching implications, as large larvae are easier to identify and can be associated with smaller unidentified specimens, allowing for improved taxonomic resolution (*sensu* Doherty *op. cit.*)

within the group. Light traps will have to be checked and cleared on a regular basis to prevent the loss of larvae to predators in the plankton which are also attracted to the device.

The continued use of drogues is also seen as an integral part of determining the function of the TNP with respect to ichthyoplankton movements. Recently, the SFRI has moored a current meter and an ADCP on Middlebank. The data from these instruments, together with the drogue data should provide a more complete picture of the current patterns in the area. This will allow us to approach the problematical issue of larval dispersal and retention with more confidence.

Amongst the criteria suggested for the design and allocation of MPA's is taking species' life histories into account since one of the chief aims of MPA's is the export of biomass (juveniles and adults) and propagules (pelagic eggs and larvae) to regions plagued by over-exploitation (Dugan & Davis 1993; Attwood *et al.* 1997). The enhanced egg (and larval) production which arises from an unfished spawner stock comprised of larger individuals (Roberts & Polunin 1993a, b) is also a common rationale invoked in favour of MPA's. The potential for dispersal of the pelagic early life history stages from reserves has been recognised (Roberts & Polunin *op. cit.*) and it has been suggested that emphasis be placed on research whose aims are to evaluate this. Hockey and Buxton (1989), in their chapter entitled *Conserving Biotic Diversity on Southern Africa's Coastline*, state one of the research priorities for the future as being: **"Establishing dispersal patterns and immigration rates of exploited organisms with a view to optimising the effectiveness of a (marine) reserve network."** It is therefore imperative, now nine years down the road, to heed this advice and determine the extent to which the TNP is benefiting nearby fisheries through ichthyoplankton dispersal as well as the processes involved. An understanding of these processes as well as information such as that gathered during this study is fundamental to the understanding of the effectiveness of MPA's. This could ultimately be incorporated into the modelling of the effective sizes and frequency of reserves along the coast such that maximum protection is afforded the spawner stock while at the same time maximum benefit is derived by neighbouring fisheries.

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APPENDICES

Appendix 1 - Catch composition and egg & species concentrations (number of larvae or eggs per m^3 of water sampled) from three replicate bongo tows performed at sunrise, day, sunset and night at Middlebank on March 28 1994 from *Natpark Aonyx*.

FAMILY	SPECIES	TOW #	LARVAL CONCENTRATION			
			SUNRISE	LIGHT	SUNSET	DARK
Clupeidae	*E. whiteheadi*	2	0.0102			0.0046
		3			0.0027	
Engraulidae	*E. japonicus*	1	0.0208			
		2		0.0036		
Bregmacerotidae	*B. atlanticus*	1				0.0057
		2				0.0092
Merlucciidae	*M. capensis*	2				0.0046
Tetrarogidae	*C. gymnoderma*	1		0.0073		
		2		0.0036		
		3		0.0077		0.0025
Blenniidae	*P. pilicornis*	3	0.0037			
	S. emarginata	3				0.0025

Totals	1	0.0208	0.0073	0.0000	0.0057
	2	0.0102	0.0073	0.0000	0.0184
	3	0.0037	0.0077	0.0027	0.0050
	Total	0.0106	0.0074	0.0011	0.0088
Eggs	1	1.5945	3.9098	2.3677	4.0151
	2	1.8460	3.9231	4.0124	3.0035
	3	1.0302	2.3302	2.5261	2.0358
	Total	1.4898	3.4074	2.9085	2.7391

Appendix 2 - Mean size, size range and percentage flexion of the catch from three replicate bongo tows performed at sunrise, day, sunset and night at Middlebank on March 28 1994 from *Natpark Aonyx* (* catch comprised a single specimen only).

FAMILY	SPECIES	TOW #	MEAN SIZE (MM)				SIZE RANGE (MM)				% FLEXION			
			SUNRISE	LIGHT	SUNSET	DARK	SUNRISE	LIGHT	SUNSET	DARK	S/RISE	LIGHT	S/SET	DARK
Clupeidae	*E. whiteheadi*	2	14.7 +- 3.05			13.67*	11.38 - 17.37				66.6			100
		3			12.15*								100	
Engraulidae	*E. japonicus*	1	24.19 +- 6.56				15.85 - 31.86				100			
		2		7.4*								0		
Bregmacerotidae	*B. atlanticus*	1				18.86*								100
		2				21.6 +- 8.7				15.49 - 27.77				100
Merlucciidae	*M. capensis*	2				5.1*								0
Tetrarogidae	*C. gymnoderma*	1		3.3 +- 0.14				3.2 - 3.4				0		
		2		4.1*								0		
		3		2.96 +- 0.2		3.5*		2.82 - 3.1				0		0
Blenniidae	*P. pilicornis*	3	3.4*								0			
	S. emarginata	3				17.36*								100

Appendix 3 - Catch composition and egg & species concentrations (number of larvae or eggs per m^3 of water sampled) from three replicate bongo tows performed at midday and after dark at Middlebank on August 29 1994 from *Natpark Aonyx*.

FAMILY	SPECIES	TOW #	LARVAL CONCENTRATION	
			MIDDAY	NIGHT
Clupeidae	*E. whiteheadi*	1		0.026249
		2		0.020986
		3		0.010783
	S. sagax	1	0.006032	0.068249
		2		0.094439
		3	0.006288	0.091654
Engraulidae	*E. japonicus*	3		0.005391
Blenniidae	*P. pilicornis*	1	0.012065	
		2		0.010493
		3		0.016174
	Species 5	3	0.006288	0.010783
	Species 4	1	0.018097	0.021000
		2		0.005247
		3	0.018863	0.032349
Gadidae	*G. capensis*	2	0.006911	
		3	0.006288	
Sparidae	*A. argyrozona*	3		0.005391
	D. s. capensis	1		0.005250
		3		0.005391
	S. salpa	2		0.005247
		3		0.005391
	Species 3	3	0.006288	
Gobiidae	Species 3	1		0.005250
Gobiesocidae	Species 1	1		0.010500
		3		0.010783
	Species 2	2		0.005247
Tetrarogidae	*C. gymnoderma*	1		0.005250
Cynoglossidae	*C. zanzibarensis*	1		0.005250
		3		0.005391
Soleidae	*A. pectoralis*	1		0.005250
		2		0.005247
Haemulidae	*P. olivaceum*	2		0.005247
	Totals	1	0.042227	0.152247
		2	0.006911	0.152151
		3	0.044014	0.199482
		Total	0.031949	0.167679
	Eggs	1	1.001387	0.881982
		2	1.057433	1.101784
		3	0.987173	0.916541
		Total	1.013845	0.967241

Appendix 4 - Mean size, size range and percentage flexion of the catch from three replicate bongo tows performed at midday and after dark at Middlebank on August 29 1994 from *Natpark Aonyx* (* catch comprised a single specimen only).

FAMILY	SPECIES	TOW #	MEAN LENGTH (MM)		SIZE RANGE (MM)		% FLEXION	
			MIDDAY	NIGHT	MIDDAY	NIGHT	MIDDAY	NIGHT
Clupeidae	*E. whiteheadi*	1		15.27 +- 1.55		12.72 - 16.51		100
		2		12.64 +- 2.75		8.64 - 14.63		75
		3		12.14 +- 2.97		10.04 - 14.24		50
	S. sagax	1	9.23*	14.13 +- 3.0		10.24 - 18.66	0	100
		2		10.68 +- 2.38		6.52 - 14.53		55.6
		3	9.52*	11.76 +- 2.12		7.35 - 15.13	0	64.7
Engraulidae	*E. japonicus*	3		5.75*				0
Blenniidae	*P. pilicornis*	1	6.3 +- 1.13		5.5 - 7.1		50	
		2		4.23 +- 0.74		3.7 - 4.75	0	
		3		4.67 +- 1.41		3.35 - 6.15		0
	Species 5	3	2.82*	3.48 +- 0.32		3/25 - 3.7	0	0
	Species 4	1	4.9 +- 0.46	5.08 +- 0.34	4.4 - 5.3	4.6 - 5.4	0	0
		2		4.4*			0	
		3	5.74 +- 1.08	5.63 +- 0.74	4.5 - 6.5	4.8 - 6.7	0	0
Gadidae	*G. capensis*	2	3.42*				0	
		3	5.6*				0	
Sparidae	*A. argyrozona*	3		4.4*				0
	D. s. capensis	1		3.7*				0
		3		2.8*				0
	S. salpa	2		8.93*				100
		3		6.55*				0
	Species 3	3	4.0*				0	
Gobiidae	Species 3	1		11.64*				100
Gobiesocidae	Species 1	1		4.4 +- 0.99		3.7 - 5.1		0
		3		4.3 +- 1.27		3.4 - 5.2		0
	Species 2	2		4.9*				0
Tetrarogidae	*C. gymnoderma*	1		4.6*				0
Cynoglossidae	*C. zanzibarensis*	1		5.1*				0
		3		4.05*				0
Soleidae	*A. pectoralis*	1		3.3*				0
		2		3.21*				0
Haemulidae	*P. olivaceum*	2		5.9*				0

Appendix 5 - Catch composition and egg & species concentrations (number of larvae or eggs per m^3 of water sampled) from three replicate bongo tows performed at sunrise, midday and sunset off Elands River on November 3, 1994 during voyage #15 of the R.S. *Algoa*.

FAMILY	SPECIES	TOW #	LARVAL CONCENTRATION		
			SUNRISE	MIDDAY	SUNSET
Clupeidae	*E. whiteheadi*	1		0.006661	
		2			0.023456
		3			0.035010
	S. sagax	1	0.069869	0.086597	0.025315
		2	0.162146	0.043218	
		3	0.128318	0.086511	0.081690
Engraulidae	*E. japonicus*	1	0.558952	0.173195	0.075945
		2	0.132665	0.253133	0.007819
		3	0.368915	0.159713	0.035010
Cynoglossidae	*C. zanzibarensis*	1	0.122271	0.219824	0.107588
		2	0.044222	0.067914	0.109461
		3	0.160398	0.126439	0.268409
Soleidae	*A. pectoralis*	1	0.052402	0.026645	0.069616
		2	0.191627	0.012348	0.054730
		3	0.152378	0.026619	0.105030
Callionymidae	*P. costatus*	1	0.052402		
		2	0.014741		
		3	0.040099		
Blenniidae	*P. pilicornis*	1		0.006661	0.018986
		2		0.012348	
		3	0.008020		
	Species 5	1	0.017467	0.006661	
		3		0.006655	
	Species 4	1			0.006329
		2			0.007819
		3	0.008020		0.011670
Tetrarogidae	*C. gymnoderma*	1	0.017467		0.018986
		2	0.014741		
Gobiidae	Species 1	1	0.017467	0.006661	0.006329
		2	0.014741		
		3		0.026619	0.046680
Sparidae	*C. laticeps*	2		0.006174	
	S. emarginatum	1		0.006661	
		2		0.006174	0.007819
		3	0.008020		0.011670
	Species 3	1	0.017467		
	Species 6	3			0.023340
	P.b. natalensis	1			
		2	0.014741		
		3			
Merlucciidae	*M. capensis*	2	0.088443		
		3	0.008020		
Carangidae	*T. trachurus*	2		0.006174	
Mugilidae	*M. cephalus*	3			0.023340
Gonorhynchidae	*G. gonorhynchus*	3			0.011670
Cheilodactylidae	Species 1	3			0.011670
Gobiesocidae	Species 1	3			0.011670

Appendix 5 continued.

Totals	1	0.925764	0.539568	0.329093
	2	0.678066	0.407483	0.211102
	3	0.882188	0.432555	0.676858
	Total	0.836736	0.458517	0.368587
Eggs	1	1.449782	1.165734	1.822669
	2	0.958137	1.074273	1.313526
	3	1.251103	1.284355	4.597969
	Total	1.217071	1.172247	2.286852

Appendix 6 - Mean size, size range and percentage flexion of the catch from three replicate bongo tows performed at sunrise, midday and sunset off Elands River on November 3, 1994 during cruise #15 of the *R.S. Algoa* (* catch comprised a single specimen only).

FAMILY	SPECIES	MEAN SIZE (MM)			SIZE RANGE (MM)			% FLEXION		
		SUNRISE	MIDDAY	SUNSET	SUNRISE	MIDDAY	SUNSET	SUNRISE	MIDDAY	SUNSET
Clupeidae	*E. whiteheadi*		8.73*						0	
				10.39 +- 5.25			6.67 - 14.1			33.3
				8.7 +- 6.32			5.0 - 16.0			33.3
	S. sagax	8.51 +- 1.9	6.2 +- 2.32	7.91 +- 2.57	6.6 - 11.13	3.5 - 12.74	6.2 - 11.73	25	7.7	25
		6.55 +- 1.26	7.79 +- 1.52		4.3 - 8.1	6.35 - 10.26		0	0	
		8.15 +- 2.42	7.05 +- 1.26	7.23 +- 4.09	5.6 - 13.12	4.0 - 8.9	2.81 - 13.16	12.5	0	28.6
Engraulidae	*E. japonicus*	8.47 +-1.67	7.5 +- 2.17	8.01 +- 1.95	6.0 - 13.23	3.6 - 12.76	5.3 - 11.97	25	11.5	8.3
		7.19 +- 1.3	6.94 +- 1.47	6.8*	5.3 - 9.3	3.0 - 9.3		0	0	0
		8.22 +- 1.7	7.28 +- 2.19	8.37 +- 2.3	5.4 - 13.03	3.7 - 12.8	6.45 - 10.92	4.35	4.2	33.3
Cynoglossidae	*C. zanzibarensis*	4.07 +- 1.41	3.7 +- 0.71	4.64 +- 1.52	2.4 - 6.5	2.3 - 5.3	3.1 - 9.57	0	0	5.9
		3.58 +- 1.42	4.5 +- 1.22	3.96 +- 1.31	2.55 - 5.2	2.5 - 7.0	1.3 - 6.15	0	0	0
		4.06 +- 1.28	4.46 +- 1.73	3.79 +- 1.39	2.3 - 8.16	2.85 - 10.06	1.55 - 8.1	5	5.3	4.3
Soleidae	*A. pectoralis*	3.37 +- 1.33	2.35 +- 0.57	2.34 +- 0.32	2.5 - 4.9	1.6 - 2.8	1.8 - 2.7	33.3	0	0
		2.63 +- 0.44	2.25 +- 0.35	3.02 +- 1.16	1.8 - 3.6	2.0 - 2.5	2.0 - 5.1	15.38	0	28.6
		2.6 +- 0.63	2.64 +- 0.46	3.19 +- 1.42	1.9 - 4.05	2.1 - 3.2	1.82 - 5.4	0	0	33.3
Callionymidae	*P. costatus*	2.2 +- 0.45			1.71 - 2.6			0		
		3.4*						0		
		2.81 +- 0.71			2.0 - 3.42			40		
Blenniidae	*P. pilicornis*		3.0*	3.18 +-0.18			3.05 - 3.3		0	0
			4.4 +- 1.56			3.3 - 5.5			50	
		5.4*						0		
	Species 5	2.1*	2.1*					0	0	
			2.5*						0	
	Species 4			3.62*						0
				4.2*						0
		5.1		4.65*				0		0
Tetrarogidae	*C. gymnoderma*	4.25*		4.96 +- 0.48			4.42 - 5.35	0		66.6
		3.5*						0		

Appendix 6 continued.

FAMILY	SPECIES	MEAN SIZE (MM)			SIZE RANGE (MM)			PERCANTAGE FLEXION		
		SUNRISE	MIDDAY	SUNSET	SUNRISE	MIDDAY	SUNSET	SUNRISE	MIDDAY	SUNSET
Gobiidae	Species 1	2.65*	1.7*	2.3*				0	0	0
		2.1*						0		
			2.07 +- 0.16	2.21 +- 0.12		1.92 - 2.3	2.05 - 2.3		0	0
Sparidae	*C. laticeps*		2.8*						0	
	S. emarginatum		4.9*						100	
			6.6*	2.4*					100	0
		5.2*		5.5*				100		100
	Species 3	3.9*						0		
	Species 6			4.78 +- 1.17			3.95 - 5.6			50
	P.b. natalensis									
		2.7*						0		
Merlucciidae	*M. capensis*	3.95 +- 1.98			2.2 - 6.8			16.7		
		5.7*						0		
Carangidae	*T. trachurus*		2.5*						0	
Mugilidae	*M. cephalus*			8.33 +- 2.58			6.5 - 10.15			100
Gonorhynchidae	*G. gonorhynchus*			71.13*						100
Cheilodactylidae	Species 1			34.62*						100
Gobiesocidae	Species 1			3.13*						0

Appendix 7 - Catch composition and egg & species concentrations (number of larvae or eggs per m^3 of water sampled) from replicate bongo tows performed at sunset and late night off Elands River between 7 & 8 October 1995 during voyage #131 of the R.S. *Africana*.

FAMILY	SPECIES	TOW#	LARVAL CONC. DAY 1		LARVAL CONC. DAY 2	
			SUNSET	MIDNIGHT	SUNSET	MIDNIGHT
Clupeidae	*E. whiteheadi*	1	0.01896	0.01411	0.10776	0.03587
		2		0.03392	0.01658	0.03241
	S. sagax	1	0.26540	0.02117		0.16399
		2	0.05450	0.12816	0.01658	0.14960
Engraulidae	*E. japonicus*	1			0.04310	
		2	0.02725	0.00377		0.00499
Cynoglossidae	*C. capensis*	1		0.00706		
	C. zanzibarensis	1	0.11374	0.01764		0.02562
		2	0.08174	0.05277	0.01658	0.05735
Soleidae	*A. pectoralis*	1		0.00353	0.02155	
	S. kleini	1	0.01896			
	H. capensis	1	0.01896			
		2		0.00377		
Callionymidae	*P. costatus*	1	0.28436	0.03881		0.18962
		2	0.05450	0.23370	0.03316	0.40641
Gobiidae	Species 1	1	0.01896	0.01764	0.04310	0.01025
		2	0.02725	0.01131	0.03316	0.00997
	Species 2	1	0.05687	0.02823		0.01537
		2		0.04146		0.04239
	Species 3	1		0.00706		
		2				0.00249
Blenniidae	*P. pilicornis*	1	0.02725			
		2			0.01658	
	Species 3	2	0.10899			
	Species 5	2	0.08174			
Triglidae	*C. capensis*	1				0.01025
		2		0.01885		0.00748
Gadidae	*G. capensis*	1			0.02155	
		2		0.00377		
Sparidae	*B. inornata*	1				0.06150
		2				0.00249
	Species 6	1				0.00256
		2	0.02725			0.00249
Carangidae	*T. trachurus*	1		0.00706		0.16143
		2		0.01508		0.03241
Scombridae	*S. japonicus*	1		0.01764		
		2		0.01131		0.02244
Gobiesocidae	Species 1	1	0.01896	0.00353	0.04310	
	Species 2	1		0.00353		
	Species 3	1			0.04310	
Ammodytidae	*G. capensis*	1	0.01896			

Appendix 7 continued.

FAMILY	SPECIES	TOW#	LARVAL CONC. DAY 1		LARVAL CONC. DAY 2	
			SUNSET	MIDNIGHT	SUNSET	MIDNIGHT
Nomeidae	Species 1	2		0.00754		
Bregmacerotidae	*B. atlanticus*	1			0.02155	
Tetrarogidae	*C. gymnoderma*	2			0.01658	
Merlucciidae	*M. capensis*	1				0.02562
		2				0.01496
Lophiidae	*L. vomerinus*	2				0.00249
Congiopodidae	*C. spinifer*	2				0.00249
Moridae	*P. capensis*	1				0.00256
		2				0.00499
Myctophidae	*D. atlanticus*	2				0.00256
	L. hectoris	2				0.00499
	S. barnardi	1				0.00512
Trichiuridae	*L. caudatus*	1				0.00769
		2				0.01247
Ophidiidae	*G. capensis*	2				0.00256
Sciaenidae	Species 1	2				0.00249
	Total larvae	1	0.83412	0.18700	0.34483	0.72516
		2	0.49046	0.62948	0.14923	0.82529
		Total	0.69312	0.40093	0.23428	0.77591
	E. japonicus eggs	1	39.12796	1.85590	2.90948	1.63225
		2	20.43597	0.65586	0.81247	1.82013
		Total	31.45892	1.27570	1.72430	1.72747
	Other eggs	1	0.24645	1.98998	0.60345	1.89873
		2	0.89918	1.79043	0.79589	1.60072
		Total	0.51425	1.89350	0.71221	1.74769
	All eggs	1	39.37441	3.84588	3.51293	3.53098
		2	21.33515	2.44629	1.60836	3.42085
		Total	31.97317	3.16919	2.43651	3.47516
Loliginidae	*L. v. reynaudii*	1	0.05687		0.02155	
		2		0.00377	0.04974	0.00997
		Total	0.03354	0.00182	0.03748	0.00505

Appendix 8 - Mean size, size range and percentage flexion of the catch from three replicate bongo tows performed at sunset and late night off Elands River between 7 & 8 October 1995 during voyage #131 of the R.S. *Africana* (* catch comprised a single specimen only).

DAY 1		TOW#	MEAN SIZE (MM)		SIZE RANGE (MM)		% FLEXION	
FAMILY	SPECIES		SUNSET	NIGHT	SUNSET	NIGHT	SUNSET	NIGHT
Clupeidae	*E. whiteheadi*	1	9.0*	13.28 +- 2.87		9.2 - 15.6	0	75
		2		11.7 +- 3.92		5.3 - 17.0		66.6
	S. sagax	1	3.1 +- 0.96	8.45 +- 4.79	2.0 - 6.0	3.1 - 13.5	0	50
		2	3.8 +- 0.42	6.77 +- 3.72	3.5 - 4.1	2.3 - 17.0	0	20.7
Engraulidae	*E. japonicus*	2	5.5*	12.4*			0	100
Cynoglossidae	*C. capensis*	1		5.2 +- 0.71		4.7 - 5.7		0
	C. zanzibarensis	1	3.18 +- 0.87	6.1 +- 2.4	2.6 - 3.6	4.0 - 9.6	0	40
		2	3.3 +- 0.56	4.42 +- 2.93	2.7 - 3.8	2.4 - 14.3	0	7.1
Soleidae	*A. pectoralis*	1		2.3*				0
	S. kleini	1	1.7*				0	
	H. capensis	1	1.9*				0	
		2		1.5*				0
Callionymidae	*P. costatus*	1	1.37 +- 0.14	2.57 +- 2.82	1.1 - 1.6	1.2 - 11.0	0	9.1
		2	1.55 +- 0.07	1.67 +- 0.33	1.5 - 1.6	1.2 - 2.5	0	0
Gobiidae	Species 1	1	2.2*	3.72 +- 0.66		2.9 - 4.4	0	40
		2	2.4*	2.87 +- 0.42		2.4 - 3.2	0	0
	Species 2	1	1.33 +- 0.06	2.25 +- 0.5	1.3 - 1.4	1.6 - 2.9	0	0
		2		2.35 +- 0.56		1.5 - 3.1		0
	Species 3	1		7.55 +- 0.21		7.4 - 7.7		100
Blenniidae	*P. pilicornis*	1	4.7*				0	
	Species 3	2	4.35 +- 0.17		4.1 - 4.5		0	
	Species 5	2	3.0 +- 0.61		2.3 - 3.4		0	
Triglidae	*C. capensis*	2		2.18 +- 0.29		1.8 - 2.5		0
Gadidae	*G. capensis*	2		2.9*				0
Sparidae	Species 6	2	4.5*				0	
Carangidae	*T. trachurus*	1		6.4 +- 0.28		6.2 - 6.6		100
		2		4.98 +- 1.73		3.6 - 7.3		25
Scombridae	*S. japonicus*	1		3.24 +- 0.05		3.2 - 3.3		0
		2		3.63 +- 0.55		3.0 - 4.0		0
Gobiesocidae	Species 1	1	2.9*	4.6*			0	0
	Species 2	1		6.8*				0
Ammodytidae	*G. capensis*	1	3.2*				0	
Nomeidae	Species 1	2		3.5 +- 0.14		3.4 - 3.6		0
Loliginidae	*L. v. reynaudii* -	1	2.43 +- 0.93		1.8 - 3.5			
	mantle length (mm)	2		2.4*				

Appendix 8 continued.

DAY 2		TOW#	MEAN SIZE (MM)		SIZE RANGE (MM)		% FLEXION	
FAMILY	SPECIES		SUNSET	NIGHT	SUNSET	NIGHT	SUNSET	NIGHT
Clupeidae	*E. whiteheadi*	1	14.72 +- 1.64	8.31 +- 3.69	12.4 - 16.5	3.0 - 13.7	100	35.7
		2	15.6*	9.27 +- 1.6		7.4 - 12.0	100	22.2
	S. sagax	1		7.77 +- 3.37		2.8 - 14.6		22.2
		2	9.3*	6.96 +- 3.44		3.0 - 18.9	100	14.3
Engraulidae	*E. japonicus*	1	3.35 +- 1.2		2.5 - 4.2		0	
		2		13.55 +- 1.91		12.2 - 14.9		100
Cynoglossidae	*C. zanzibarensis*	1		4.43 +- 1.29		3.2 - 7.6		0
		2	4.3*	4.23 +- 1.87		2.0 - 11.2	0	8.7
Soleidae	*A. pectoralis*	1	2.6*				0	
Callionymidae	*P. costatus*	1		2.02 +- 0.66		1.3 - 5.2		1.4
		2	1.95 +- 0.21	1.88 +- 0.58	1.8 - 2.1	1.1 - 5.5	0	1.2
Gobiidae	Species 1	1	4.65 +- 1.48	3.45 +- 1.29	3.6 - 5.7	2.3 - 5.3	50	25
		2	3.05 +- 0.78	4.28 +- 1.08	2.5 - 3.6	2.9 - 5.4	0	50
	Species 2	1		3.25 +- 0.7		2.7 - 4.5		16.7
		2		2.75 +- 0.24		2.3 - 3.4		0
	Species 3	2		8.3*				100
Blenniidae	*P. pilicornis*	2	5.8*				100	
Triglidae	*C. capensis*	1		3.93 +- 1.67		2.8 - 6.4		0
		2		4.23 +- 1.36		3.4 - 5.8		33.3
Gadidae	*G. capensis*	1	12.27*				100	
Sparidae	*B. inornata*	1		4.65 +- 1.73		1.9 - 8.5		25
		2		2.5*				0
	Species 6	1		5.8*				0
		2		5.1*				100
Carangidae	*T. trachurus*	1		3.6 +- 1.04		2.2 - 7.5		1.6
		2		3.86 +- 1.16		2.3 - 6.2		23.1
Scombridae	*S. japonicus*	2		5.59 +- 2.04		2.6 - 7.6		66.6
Gobiesocidae	Species 1	1	5.0 +- 0.28		4.8 - 5.2		0	
	Species 3	1	4.65 +- 0.64		4.2 - 5.2		100	
Bregmacerotidae	*B. atlanticus*	1	21.7*				100	
Tetrarogidae	*C. gymnoderma*	2	3.0*				0	
Merlucciidae	*M. capensis*	1		2.41 +- 0.7		1.8 - 3.8		0
		2		3.43 +- 0.51		2.6 - 4.0		0
Lophiidae	*L. vomerinus*	2		4.5*				0
Congiopodidae	*C. spinifer*	2		8.4*				100
Moridae	*P. capensis*	1		2.6*				0
		2		3.75 +- 1.34		2.8 - 4.7		0
Myctophidae	*D. atlanticus*	2		4.4*				0
	L. hectoris	2		4.35 +- 0.92		3.7 - 5.0		0
	S. barnardi	1		4.53 +- 0.21		4.3 - 4.8		0
Trichiuridae	*L. caudatus*	1		5.83 +- 0.32		5.6 - 6.2		0
		2		6.88 +- 0.19		6.6 - 7.1		0
Ophidiidae	*G. capensis*	2		9.4*				0
Sciaenidae	Species 1	2		3.7*				0
Loliginidae	*L. v. reynaudii*	1	3.2*					
		2	1.67 +- 0.6	2.33 +- 0.91	1.1 - 2.3	1.2 - 3.4		

Appendix 9 - Catch composition and egg & species concentrations (number of larvae or eggs per m^3 of water sampled) from replicate bongo tows performed off Bloukrans River between 25 & 26 April 1996 during voyage #135 of the R.S. *Africana*. Samples were taken at sunrise, midday, sunset and late night on the 25th, while no midday samples were taken on the 26th.

			LARVAL CONC. (DAY 1)				LARVAL CONC. (DAY 2)		
FAMILY	SPECIES	TOW#	S/RISE	DAY	S/SET	NIGHT	S/RISE	S/SET	NIGHT
Clupeidae	*E. whiteheadi*	1	0.0288	0.0053	0.0464	0.2157	0.0148	0.0076	
		2	0.0242	0.0128	0.0391	0.0565	0.0127	0.0061	
Engraulidae	*E. japonicus*	1			0.0058	0.0072		0.0076	
		2			0.0065			0.0061	
Callionymidae	*P. costatus*	1		0.0158	0.0058	0.0144		0.0307	0.0148
		2	0.0060	0.0128	0.0195	0.0242			0.0201
Sparidae	Species 10	1	0.0048						
Merlucciidae	*M. capensis*	1	0.0096	0.0263	0.0116	0.0288	0.0074	0.0076	
		2	0.0181	0.0064	0.0065			0.0246	0.0201
Gobiidae	Species 1	1	0.0048	0.0053	0.0232	0.0072			
		2		0.0064	0.0195	0.0161		0.0123	0.0067
	Species 2	1	0.0096			0.0072	0.0148		
		2	0.0181	0.0128				0.0307	0.0134
	Species 3	1	0.0240	0.0053	0.0116	0.0359			
		2	0.0060	0.0064		0.0081			0.0134
Cynoglossidae	*C. capensis*	2	0.0060		0.0065				
	C. zanzibarensis	1	0.0048	0.0128	0.0116	0.0431		0.0229	0.0074
		2	0.0060		0.0260	0.0161		0.0430	
Soleidae	*A. pectoralis*	1	0.0096	0.0053	0.0174	0.0216	0.0074		
		2		0.0128	0.0065		0.0191		0.0067
	H. capensis	1						0.0076	
		2		0.0064				0.0061	
	M. ocellatus	2				0.0161		0.0061	
Triglidae	*C. capensis*	2		0.0064					
Ophidiidae	*G. capensis*	1				0.0072			
Cheilodactylidae	Species 1	1		0.0053					
		2					0.0127		
Syngnathidae	*S. acus*	1		0.0053					
Gobiesocidae	Species 2	1				0.0072			
		2						0.0061	
	Species 3	2						0.0061	0.0134
Ammodytidae	*G. capensis*	1				0.0072			
Carangidae	*S. lalandi*	2					0.0064		
Congiopodidae	*C. spinifer*	2					0.0064		
Bregmacerotidae	*B. atlanticus*	1							0.0074

Appendix 9 continued.

			LARVAL CONC. (DAY 1)				LARVAL CONC. (DAY 2)		
FAMILY	SPECIES	TOW#	S/RISE	DAY	S/SET	NIGHT	S/RISE	S/SET	NIGHT
	Totals	1	0.1010	0.0840	0.1450	0.4026	0.0444	0.0535	0.0296
		2	0.0847	0.0833	0.1302	0.1453	0.0699	0.1781	0.0870
		Total	0.0938	0.0837	0.1380	0.2814	0.0582	0.1226	0.0598
Loliginidae	*L. v. reynaudii*	1	0.0048		0.0058	0.0072			
		2		0.0064	0.0065			0.0061	0.0067
		Total	0.0027	0.0029	0.0061	0.0038	0.0000	0.0034	0.0035
	Eggs	1	0.3942	0.2784	0.1334	0.4242	0.0593	0.4205	0.1481
		2	0.1512	0.0961	0.1497	0.1453	0.2034	0.3317	0.1472
		Total	0.2866	0.1962	0.1411	0.2928	0.1368	0.3713	0.1476

Appendix 10 - Mean size, size range and percentage flexion of the catch from replicate bongo tows performed off Bloukrans River between 25 & 26 April 1996 during cruise #135 of the *R.S. Africana*. Samples were taken at sunrise, midday, sunset and late night on the 25th, while no midday samples were taken on the 26th.

FAMILY	SPECIES	TOW #	MEAN SIZE (MM)				SIZE RANGE (MM)				% FLEXION			
DAY 1			SUNRISE	LIGHT	SUNSET	DARK	SUNRISE	LIGHT	SUNSET	DARK	S/RISE	LIGHT	S/SET	DARK
Clupeidae	*E whiteheadi*	1	13.9 +- 3.96	6.1*	14.65 +- 1.86	12.98 +- 3.2	7.7 - 17.3		13.3 - 18.9	7.6 - 18.8	83.3	0	100	80
		2	14.03 +- 0.76	13.0 +- 0.24	12.47 +- 3.81	15.46 +- 3.69	13.1 - 14.9	12.8 - 13.2	9.1 - 19.6	8.7 - 19.1	100	100	66.6	85.7
Engraulidae	*E japonicus*	1			14.5*	15.0*							100	100
		2			11.6*								100	
Callionymidae	*P costatus*	1		1.8 +- 0	2.3*	13.3 +- 1.13		All 1.8		12.5 - 14.1		0	0	100
		2	3.7*	3.55 +- 1.77	10.97 +- 2.82	10.27 +- 6.4		2.3 - 4.8	9.0 - 14.2	2.9 - 14.5	100	50	100	66.6
Sparidae	Species 10	1	5.6*								100			
Merlucciidae	*M capensis*	1	3.85 +- 1.91	2.3 +- 0.44	7.2 +- 1.84	6.05 +- 4.44	2.5 - 5.2	1.8 - 3.0	5.9 - 8.5	3.2 - 12.6	0	0	50	25
		2	3.57 +- 1.27	2.5*	8.0*		2.2 - 4.7				0	0	100	
Gobiidae	Species 1	1	2.5*	5.6*	5.3 +- 0.5	4.0*			4.8 - 5.9		0	100	100	100
		2		2.4*	3.7 +- 2.23	4.9 +- 0.85			1.9 - 6.2	4.3 - 5.5		0	33.3	50
	Species 2	1	2.7 +- 0.42			4.2*	2.4 - 3.0				0			100
		2	2.03 +- 0.32	2.8 +- 0.85			1.8 - 2.4	2.2 - 3.4			0	0		
	Species 3	1	2.72 +- 1.1	2.9*	3.8 +- 0	5.18 +- 1.56	1.4 - 4.2		All 3.8	3.8 - 7.2	20	0	0	100
		2	3.7*	4.4*		4.2*					100	100		100
Cynoglossidae	*C capensis*	2	5.0*		11.2*						0		100	
	C zanzibarensis	1	9.0*	3.6 +- 0.71	3.85 +- 0.92	7.2 +- 3.26		3.1 - 4.1	3.2 - 4.5	3.7 - 13.0	0	0	0	16.7
		2	4.4*		7.93 +- 2.26	4.85 +- 1.2			6.0 - 11.5	4.0 - 5.7	0		25	0
Soleidae	*A pectoralis*	1	2.3 +- 0.14	3.2*	3.55 +- 0.13	2.93 +- 0.4	2.2 - 2.4		3.45 - 3.7	2.7 - 3.4	0	0	0	0
		2		2.05 +- 0.21	4.5*			1.9 - 2.2				0	0	
	H capensis	2		1.8*								0		
	M ocellatus	2				4.25 +- 1.34				3.3 - 5.2				50
Triglidae	*C capensis*	2		3.6*								0		
Ophidiidae	*G capensis*	1				24.0*								100
Cheilodactylidae	Species 1	1		3.8*								0		
		2												
Syngnathidae	*S acus*	1		58.3*								100		
Gobiesocidae	Species 2	1				7.1*								100

Appendix 10 continued.

FAMILY	SPECIES	TOW #	MEAN SIZE (MM)				SIZE RANGE (MM)				PERCANTAGE FLEXION			
DAY 1			SUNRISE	LIGHT	SUNSET	DARK	SUNRISE	LIGHT	SUNSET	DARK	S/RISE	LIGHT	S/SET	DARK
Ammodytidae	*G capensis*	1				6.6*								100
Loliginidae	*L v reynaudii* -	1	3.2*		2.7*	3.3*								
	mantle length (mm)	2		2.5*	19.0*									

FAMILY	SPECIES	TOW#	MEAN SIZE (MM)			SIZE RANGE (MM)			PERCENTAGE FLEXION		
DAY 2			SUNRISE	SUNSET	NIGHT	SUNRISE	SUNSET	NIGHT	SUNRISE	SUNSET	NIGHT
Clupeidae	*E whiteheadi*	1	13.25 +- 2.47	14.0*		11.5 - 15.0			100	100	
		2	11.35 +- 2.47	17.0*		9.6 - 13.1			50	100	
Engraulidae	*E japonicus*	1		16.6*						100	
		2		19.3*						100	
Callionymidae	*P costatus*	1			13.3 +- 4.1			10.4 - 16.2			100
		2		13.88 +- 1.47	13.07 +- 1.74		11.5 - 15.5	11.1 - 14.4		100	100
Merlucciidae	*M capensis*	1	1.9*						0		
		2		6.05 +- 6.48	3.8 +- 2.86		2.3 - 15.7	2.1 - 7.1		25	33.3
Gobiidae	Species 1	2		5.3 +- 0.28	2.9*		5.1 - 5.5			100	0
	Species 2	1	2.35 +- 0.35			2.1 - 2.6			0		
		2		2.0 +- 0.4	2.45 +- 0.21		1.3 - 2.3	2.3 - 2.6		0	0
	Species 3	2			7.45 +- 0.21			7.3 - 7.6			100
Cynoglossidae	*C zanzibarensis*	1		6.37 +- 2.49	15.8*		3.5 - 8.0			0	100
		2		6.74 +- 5.3			1.5 - 16.3			28.6	
Soleidae	*A pectoralis*	1	3.7*						0		
		2	3.07 +- 0.76		4.2*	2.2 - 3.6			0		0
	H capensis	1		5.6*						100	
		2		5.0*						100	
	M ocellatus	2		6.1*						100	
Cheilodactylidae	Species 1	2	2.25 +- 0.07			2.2 - 2.3			0		
Gobiesocidae	Species 2	2		6.0*						100	
	Species 3	2		3.9*	3.98 +- 0.32			3.75 - 4.2		0	0
Carangidae	*S lalandi*	2	2.7*						0		

Appendix 10 continued.

FAMILY	SPECIES	TOW#	MEAN SIZE (MM)			SIZE RANGE (MM)			PERCENTAGE FLEXION		
DAY 2			SUNRISE	SUNSET	NIGHT	SUNRISE	SUNSET	NIGHT	SUNRISE	SUNSET	NIGHT
Congiopodidae	*C. spinifer*	**2**	2.5*						0		
Bregmacerotidae	*B. atlanticus*	**1**			24.9*						100
Loliginidae	*L. v. reynaudii* - mantle length (mm)	**2**		1.5*	2.1*						

Appendix 11 - A list of fish larvae and squid para-larvae caught at Middlebank (M) and all stations combined for the period between August 1993 and October 1996, which were not present in sufficient concentrations or frequently enough for statistical analysis.

		DATE - CONCENTRATION (#/m³)	
FAMILY	SPECIES	MIDDLEBANK	COMBINED STATIONS
Gonorhynchidae	*Gonorhynchus gonorhynchus*	03/11/94 - 0.00029	
Myctophidae	*Symbolophorus barnardi*		07/10/95 - 0.0013
	Hygophum sp		25/07/95 - 0.0006 15/08/95 - 0.00071
	Diogenichthys atlanticus		19/08/93 - 0.00026 07/10/95 - 0.00065
Moridae	*Physiculus capensis*		07/10/95 - 0.00195
Bregmacerotidae	*Bregmaceros atlanticus*	28/03/94 - 0.00039 25/04/96 - 0.0008	07/10/95 - 0.00065 25/04/96 - 0.00046
Ophidiidae	*Genypterus capensis*	19/08/93 - 0.00075	19/08/93 - 0.00026 07/10/95 - 0.00065 25/04/96 - 0.00046
Lophiidae	*Lophius upsicephalus*		07/10/95 - 0.00065
Gobiesocidae	Species 3	25/04/96 - 0.0024	07/10/95 - 0.0013 25/04/96 - 0.00138
Zeidae	*Zeus faber*	19/08/93 - 0.0022 20/06/95 - 0.0061	19/08/93 - 0.00078 20/06/95 - 0.00159 20/07/96 - 0.00097
Syngnathidae	*Syngnathus acus*		15/08/95 - 0.00071 25/04/96 - 0.00046
Congiopodidae	*Congiopodus spinifer*	25/04/96 - 0.0008	07/10/95 - 0.00065 25/04/96 - 0.00046
Serranidae	*Serranus cabrilla*	19/08/93 - 0.00075	19/08/93 - 0.00026
Sparidae	*Boopsoidea inornata*		07/10/95 - 0.01627
	Diplodus cervinus hottentotus		22/11/95 - 0.00062
	Sarpa salpa	24/05/94 - 0.00085 29/08/94 - 0.00072	24/11/93 - 0.0012 22/11/95 - 0.00062
	Species 3	03/11/94 - 0.00029	19/08/93 - 0.00052 24/11/93 - 0.0012
	Species 6	03/11/94 - 0.00058 30/01/96 - 0.0032	25/04/95 - 0.00076 07/10/95 - 0.00195 22/11/95 - 0.00062 30/01/96 - 0.0016
	Species 10	25/04/96 - 0.0008	24/11/93 - 0.0012 09/03/96 - 0.00054 25/04/96 - 0.00046
	Species 12		15/08/95 - 0.00071 22/11/95 - 0.00062
	Species 13	20/06/95 - 0.0061	20/06/95 - 0.00159
Monodactylidae	*Monodactylus falciformis*		16/02/95 - 0.00137
Sciaenidae	*Atractoscion aequidens*		24/11/93 - 0.0012 22/11/95 - 0.00125 09/03/96 - 0.00054
	Species 1		16/02/95 - 0.00137 15/08/95 - 0.00071
	Species 2		07/10/95 - 0.00065

Appendix 11 continued.

		DATE - CONCENTRATION (#/m^3)	
FAMILY	SPECIES	MIDDLEBANK	COMBINED STATIONS
Carangidae	*Seriola lalandi*	25/04/96 - 0.0008	25/04/96 - 0.00046
Cheilodactylidae	*Cheilodacthylus fasciatus*	19/08/93 - 0.00224 25/07/95 - 0.00239	19/08/93 - 0.00078 25/07/95 - 0.0006 15/08/95 - 0.00425
	Chirodactylus brachdactylus		03/11/94 - 0.00293
	Species 2		20/06/95 - 0.0048 15/08/95 - 0.00212
Mugilidae	*Mugil cephalus*	03/11/94 - 0.00059	
	Liza richardsoni		24/11/93 - 0.0012 22/11/95 - 0.00062
	Species 3		24/11/93 - 0.0012 16/02/95 - 0.00137
Champsodontidae	*Champsodon capensis*		07/10/95 - 0.00065
Blenniidae	*Scartella emarginata*	28/03/94 - 0.00013	24/11/93 - 0.0143
	Species 3		19/08/93 - 0.00026 24/11/93 - 0.0024 07/10/95 - 0.0026
	Species 6	20/07/96 - 0.0019	15/08/95 - 0.0014 20/07/96 - 0.00097
Gobiidae	Species 2	24/05/94 - 0.00085 25/04/96 - 0.0113 20/07/96 - 0.0014	19/08/93 - 0.00052 07/10/95 - 0.0293 25/04/96 - 0.0078 20/07/96 - 0.00073
	Species 3	29/08/94 - 0.00036 25/04/96 - 0.0064	20/06/95 - 0.0016 15/08/95 - 0.00071 07/10/95 - 0.00195 25/04/96 - 0.00826
	Species 4		19/08/93 - 0.00026
Ammodytidae	*Gymnammodytes capensis*	30/01/96 - 0.0016	30/01/96 - 0.00079 25/04/96 - 0.00046
Gempylidae	*Thyrsites atun*	19/08/93 - 0.00823	19/08/93 - 0.00549 25/07/95 - 0.0012
Trichiuridae	*Lepidopus caudatus*	07/10/95 - 0.00521	25/04/95 - 0.00076 15/08/95 - 0.00071
Scombridae	*Scomber japonicus*	19/08/93 - 0.00673	15/08/95 - 0.00071 07/10/95 - 0.01107
Cynoglossidae	*Cynoglossus capensis*	25/04/96 - 0.0008	25/07/95 - 0.0006 15/08/95 - 0.00071 07/10/95 - 0.0013 25/04/96 - 0.00997
Soleidae	*Monochirus ocellatus*	25/04/96 - 0.0008	25/04/96 - 0.00138
	Solea bleeken	09/03/96 - 0.00147	09/03/96 - 0.00054
	Synaptunichthys kleini	25/04/95 - 0.00345	25/04/95 - 0.00076 07/10/95 - 0.00065
Bothidae	*Arnoglossus capensis*		15/08/95 - 0.00071
Loliginidae	*Loligo vulgaris reynaudii*	25/04/96 - 0.00241	19/08/93 - 0.00183 07/10/95 - 0.00781 25/04/96 - 0.00321

Appendix 12 - Concentrations (larvae/m³) of fish larvae caught along an offshore transect off Storms River mouth between January 1995 and May 1996. Only those species present frequently enough or in sufficiently high concentrations for statistical analysis have been included. The numbers 5, 10 & 15 indicate the distance in nautical miles from Storms River mouth, while M denotes Middlebank.

	Sardinops sagax				*Etrumeus whiteheadi*				*Engraulis japonicus*				*Lampanyctodes hectoris*			
Date / Station	15	10	5	M	15	10	5	M	15	10	5	M	15	10	5	M
Jan 95	0	0	0	0	0	0	0	0	0.2831	0.2321	0.1803	0.0211	0	0	0	0
Feb 95	0.0019	0.0139	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar 95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apr 95	0	0	0.0103	0	0	0	0	0	0	0.0019	0.0041	0	0	0	0.0021	0
Jun 95	0	0.0239	0.0058	0.0486	0	0	0.0173	0.0122	0	0	0	0.0122	0	0	0.0115	0
Jul 95	0	0.1489	0.0152	0.0191	0	0	0	0	0	0.0015	0	0	0	0.0338	0	0
Aug 95	0	0.1689	0.1577	0.017	0	0.0021	0	0	0	0	0	0	0	0.0082	0	0
Nov 95	0	0.0017	0.0019	0.004	0	0	0	0.002	0	0.0017	0.0038	0.004	0	0	0	0
Jan 96	0	0	0.0015	0.0048	0	0	0	0	0	0	0.0031	0.0258	0	0	0	0
Feb 96	0	0	0.0036	0	0	0	0	0.002	0	0.0067	0	0.004	0	0	0	0
Mar 96	0	0.0136	0.0017	0	0	0	0	0	0	0.0051	0.0052	0	0	0.0017	0	0
May 96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Galeichthys capensis				*Cheilodactylichthys capensis*				*Argyrozona argyrozona*				*Diplodus sargus capensis*			
Date / Station	15	10	5	M	15	10	5	M	15	10	5	M	15	10	5	M
Jan 95	0	0	0	0	0	0.0042	0.0021	0	0	0	0	0	0	0	0	0
Feb 95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar 95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apr 95	0	0	0.0019	0	0	0	0	0	0	0	0	0.0035	0	0	0	0
Jun 95	0	0.0034	0	0	0	0	0	0	0	0	0	0.0182	0	0	0	0.0061
Jul 95	0	0.0184	0.0084	0.0072	0	0.0276	0.0101	0.0048	0	0	0	0	0	0.0077	0.0034	0
Aug 95	0	0.0041	0.0131	0.0064	0	0.0165	0.0591	0	0	0	0.0022	0.0043	0	0.0021	0.0241	0
Nov 95	0	0	0	0	0	0.0017	0.0019	0	0	0	0.0038	0	0	0	0	0
Jan 96	0	0	0	0	0	0	0	0	0	0	0	0.0032	0	0	0	0
Feb 96	0	0	0	0	0	0	0	0.002	0	0	0	0	0	0	0	0
Mar 96	0	0	0	0.0015	0	0.0034	0.0017	0	0	0.0017	0	0	0	0.0017	0	0
May 96	0	0	0	0.0021	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 12 continued.

Date / Station	*Chrysoblephus laticeps*				*Pagellus bellottii natalensis*				Sparidae Sp11				*Trachurus trachurus*			
	15	10	5	M	15	10	5	M	15	10	5	M	15	10	5	M
Jan 95	0	0	0	0	0.004	0	0.0021	0	0	0.0021	0	0	0	0	0	0
Feb 95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar 95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apr 95	0	0	0	0	0	0	0	0	0	0.0056	0.0021	0	0	0	0	0
Jun 95	0	0	0	0	0	0	0	0.0061	0	0	0	0	0	0	0	0.0182
Jul 95	0	0	0	0	0	0.0015	0.0017	0.0048	0		0.037	0.0717	0	0.066	0.0017	0.0024
Aug 95	0	0.0021	0	0	0	0.0082	0.0066	0	0	0	0.0066	0	0	0.0185	0.035	0.0021
Nov 95	0	0.0034	0.0038	0	0	0	0	0	0	0	0	0	0	0.0017	0	0.002
Jan 96	0	0	0	0	0	0	0	0.0016	0	0	0	0	0	0	0	0
Feb 96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar 96	0	0.0017	0	0	0	0.0068	0.0017	0	0	0	0	0	0	0.0034	0	0
May 96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Date / Station	Chellodactylidae Sp1				*Parablennius pilicornis*				*Paracallionymus costatus*				*Cynoglossus zanzibarensis*			
	15	10	5	M	15	10	5	M	15	10	5	M	15	10	5	M
Jan 95	0	0	0	0	0	0	0	0.0033	0	0	0	0.0016	0.012	0.0125	0.0021	0.0016
Feb 95	0	0	0	0	0.0136	0	0	0	0	0	0	0	0	0	0	0
Mar 95	0	0	0	0	0	0	0	0.0027	0	0	0	0	0	0	0	0.0027
Apr 95	0	0.0019	0.0021	0	0	0	0	0	0	0.0056	0	0	0	0	0.0021	0.038
Jun 95	0	0	0	0.0061	0	0.0034	0.0058	0	0	0	0	0	0	0	0.0058	0
Jul 95	0	0.0353	0.0034	0	0	0	0	0	0	0	0	0	0	0	0	0
Aug 95	0	0.0371	0.0066	0.0043	0	0.0021	0.0024	0	0	0.0124	0.0066	0	0	0.0041	0.0088	0
Nov 95	0	0	0	0	0	0	0.0038	0.012	0	0	0	0	0	0.0034	0	0
Jan 96	0	0	0	0	0	0	0.0015	0.0016	0	0	0	0	0	0	0	0
Feb 96	0	0	0	0	0	0	0	0	0	0.0067	0	0.006	0	0	0	0
Mar 96	0	0	0	0	0	0	0	0	0	0	0	0.0029	0	0	0	0
May 96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 12 continued.

	Austroglossus pectoralis			
Date / Station	15	10	5	M
Jan 95	0	0	0.0043	0
Feb 95	0	0	0	0
Mar 95	0	0	0	0
Apr 95	0	0	0	0.0173
Jun 95	0	0	0	0
Jul 95	0	0	0	0
Aug 95	0	0	0.0066	0
Nov 95	0	0.0086	0	0
Jan 96	0	0	0	0
Feb 96	0	0	0	0.006
Mar 96	0	0	0	0
May 96	0	0	0	0

Appendix 13 - Concentrations (larvae/m³) of fish larvae caught along an offshore transect off Storms River mouth between January 1995 and May 1996, which were not present frequently enough or in sufficiently high concentrations for statistical analysis. The distances in miles indicate the distance offshore from Storms River mouth.

		Sample Date - Concentration (#/m³)			
FAMILY	SPECIES	MIDDLEBANK	5 MILES	10 MILES	15 MILES
Myctophidae	*Hygophum sp.*		Aug '95 - 0.0022	July '95 - 0.0015	
Merlucciidae	*Merluccius capensis*			Aug '95 - 0.0021 Feb '96 - 0.0017	
Zeidae	*Zeus faber*	June '95 - 0.0061			
Syngnathidae	*Syngnathus acus*			Aug '95 - 0.0021	
Tetrarogidae	*Coccotropsis gymnoderma*	May '96 - 8.65E-05	Aug '95 - 0.0044 Mar '96 - 0.0018 May '96 - 0.0016		Feb '95 - 0.0019
Haemulidae	*Pomadasys olivaceum*		Jul ' 95 - 0.0051	Aug ' 95 - 0.0124 Mar ' 96 - 0.0034	
Sparidae	*Diplodus cervinus hottentotus*		Nov '95 - 0.0019		
	Sarpa salpa			Nov '95 - 0.0017	
	Species 6	Jan '96 - 0.0032	Apr '95 - 0.0021	Nov '95 - 0.0017	
	Species 10			Mar '96 - 0.0017	
	Species 12		Aug '95 - 0.0022 Nov '95 - 0.0019		
	Species 13	Jun '95 - 0.0061			
Monodactylidae	*Monodactylus falciformis*				Feb '95 - 0.0019
Scombridae	*Scomber japonicus*			Aug '95 - 0.0021	
Sciaenidae	*Atractoscion aequidens*		Mar '96 - 0.0017	Nov '95 - 0.00345	
Cheilodactylidae	Species 2		Aug '95 - 0.0066	Jun '95 - 0.0103	
	Cheilodactylus fasciatus	Jul '95 - 0.0024	Aug '95 - 0.0066		
Mugilidae	*Liza richardsoni*		Nov '95 - 0.0019		
	Species 3				Feb '95 - 0.0019
Blenniidae	Species 4	Aug '95 - 0.0021			Feb '95 - 0.0019
	Species 5	Jan '95 - 0.0008 Jan '96 - 0.0048		Jan '95 - 0.0021	Feb '95 - 0.0019
	Species 6			Aug '95 - 0.0041	
Ammodytidae	*Gymnammodytes capensis*	Jan '96 - 0.0016			
Gobiidae	Species 1	Nov '95 - 0.002		Aug '95 - 0.0082 Nov '95 - 0.0017	
	Species 3			Jun '95 - 0.0034 Aug '95 - 0.0021	
Gempylidae	*Thyrsites atun*			Jul '95 - 0.0031	
Trichiuridae	*Lepidopus caudatus*			Apr '95 - 0.0019 Aug '95 - 0.0021	
Cynoglossidae	*Cynoglossus capensis*		Jul '95 - 0.0015 Aug '95 - 0.0021		
Bothidae	*Arnoglossus capensis*		Aug '95 - 0.0022		
Soleidae	*Heteromycteris capensis*	Feb '96 - 0.002		Nov '95 - 0.0034 Feb '96 - 0.0017	
	Solea bleekeri	Mar '96 - 0.0015			
	Synapturichthys kleini	Apr '95 - 0.0035			

Appendix 14 - Monthly concentrations of fish larvae and squid para-larvae (#/m³) caught at Middlebank (M) and at all stations combined (O) during the period August 1993 to October 1996.

	E. japonicus		*E. whiteheadi*		*S. sagax*		*G. capensis*		*M. capensis*		*L. hectoris*		Gobiesocidae Sp1		Gobiesocidae Sp2		*C. gymnoderma*	
	M	O	M	O	M	O	M	O	M	O	M	O	M	O	M	O	M	O
Aug 93	0	0.0057	0.0194	0.0703	2.9197	1.2794	0.0142	0.0086	0.006	0.0068	0	0	0	0.046254	0	0.004181	0	0
Nov 93	0	0.055	0	0.0801	0	0.0382	0	0	0	0	0	0	0	0.010756	0	0	0	0.01434
Feb 94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar 94	0.0007	0	0.0007	0	0	0	0	0	0.0001	0	0	0	0	0	0	0	0.00078	0
May 94	0.0248	0	0	0	0.0009	0	0.0009	0	0	0	0	0	0	0	0	0	0	0
Aug 94	0.0004	0	0.0043	0	0.0183	0	0.0007	0	0	0	0	0	0.001438	0	0.00036	0	0.00036	0
Sep 94	0	0	0.0012	0	0.0075	0	0.0006	0	0	0	0	0	0	0	0	0	0	0
Nov 94	0.0572	0	0.0023	0	0.022	0	0	0	0.0021	0	0	0	0.000293	0	0	0	0.00147	0
Dec 94	0.0022	0	0	0	0.0007	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan 95	0.0211	0.0939	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feb 95	0	0	0	0	0	0.0055	0	0	0	0	0	0	0	0	0	0	0	0.00137
Mar 95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apr 95	0	0.0023	0	0	0	0.0038	0	0.0008	0	0	0	8E-04	0	0	0	0	0	0
Jun 95	0.0122	0.0032	0.0122	0.0079	0.0486	0.0254	0	0.0016	0	0	0	0.003	0	0	0	0	0	0
Jul 95	0	0.0006	0	0	0.0191	0.0685	0.0072	0.012	0	0	0	0.013	0	0	0	0	0	0
Aug 95	0	0	0	0.0007	0.017	0.1147	0.0064	0.0078	0	0.0007	0	0.003	0	0	0	0	0	0.00142
Oct 95	0	0.0052	0	0.0299	0	0.1172	0	0.0013	0	0.0104	0	0.001	0	0.002604	0	0.000651	0	0.00065
Nov 95	0.004	0.0031	0.002	0.0006	0.004	0.0025	0	0	0	0	0	0	0	0	0	0	0	0
Jan 96	0.0258	0.0142	0	0	0.0048	0.0031	0	0	0	0	0	0	0	0	0	0	0	0
Feb 96	0.004	0.0036	0.002	0.0006	0	0.0012	0	0	0	0.0006	0	0	0	0	0	0	0	0
Mar 96	0	0.0033	0	0	0	0.0049	0.0015	0.0005	0	0	0	5E-04	0	0	0	0	0	0.00054
Apr 96	0.0016	0.0023	0.0129	0.0321	0	0	0	0	0.0105	0.0119	0	0	0	0	0.000804	0.000918	0	0
May 96	0	0	0	0	0	0	0	0.0007	0	0	0	0	0	0	0	0	8.7E-05	0.00202
Jul 96	0.0019	0.0029	0	0	0.0271	0.0319	0.0019	0.0019	0	0.001	0	1E-03	0	0	0	0	0	0
Oct 96	0.0028	0.005	0	0	0.0014	0.003	0	0	0	0	0	0	0	0	0	0	0	0.00101

Appendix 14 continued.

	C. capensis		*P. olivaceum*		*A. argyrozona*		*D. a. capensis*		*C. laticeps*		*P. b. natalensis*		*S. emarginatum*		Sparidae Sp11		*T. trachurus*	
	M	O	M	O	M	O	M	O	M	O	M	O	M	O	M	O	M	O
Aug 93	0.006	0.0024	0.00224	0.00183	0.0613	0.0267	0.0217	0.0209	0.0015	0.0031	0.003	0.001	0	0	0.0007	0.0003	0.9588	0.415
Nov 93	0	0.0012	0	0	0	0.0048	0	0.0012	0	0.0012	0	0	0	0.00478	0	0	0	0
Feb 94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar 94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May 94	0.0009	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aug 94	0	0	0.00036	0	0.0004	0	0.0007	0	0	0	0	0	0	0	0	0	0	0
Sep 94	0	0	0	0	0.0006	0	0.0012	0	0	0	0	0	0	0	0.0006	0	0	0
Nov 94	0	0	0	0	0	0	0	0	0.0003	0	0	0	0	0.00147	0	0	0.0003	0
Dec 94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jan 95	0	0.0011	0	0	0	0	0	0	0	0	0	0.0011	0	0	0	0.0004	0	0
Feb 95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar 95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apr 95	0	0	0	0	0.0035	0.0008	0	0	0	0	0	0	0	0	0	0.0031	0	0
Jun 95	0	0	0	0	0.0182	0.0048	0.0061	0.0016	0	0	0.0061	0.0016	0	0	0	0	0.0182	0.0048
Jul 95	0.0048	0.0156	0	0.0018	0	0	0	0.0042	0	0	0.0048	0.0024	0	0	0.0717	0.1941	0.0024	0.027
Aug 95	0	0.0248	0	0.00425	0.0043	0.0021	0	0.0085	0	0.0007	0	0.005	0	0	0	0.0021	0.0021	0.0184
Oct 95	0	0.0078	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0534
Nov 95	0	0.0012	0	0	0	0.0012	0	0	0	0.0025	0	0	0.01395	0.00748	0	0	0.002	0.0012
Jan 96	0	0	0	0	0.0032	0.0016	0	0	0	0	0.0016	0.0008	0	0	0	0	0	0
Feb 96	0.002	0.0006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mar 96	0	0.0016	0	0.00109	0	0.0005	0	0.0005	0	0.0005	0	0.0027	0	0	0	0	0	0.0011
Apr 96	0	0.0005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May 96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul 96	0	0.0019	0.00193	0.00097	0.0019	0.001	0.0039	0.0029	0	0	0	0.001	0	0	0	0.001	0	0
Oct 96	0	0	0	0	0	0	0	0	0.0014	0.002	0	0	0	0	0	0	0	0

Appendix 14 continued.

	Chellodactylidae Sp1		*P. pilicornis*		Blennilidae Sp4		Blennilidae Sp5		*P. costatus*		Gobiidae Sp1		Gobiidae Sp2		Gobiidae Sp3		*C. zanzibarensis*	
	M	O	M	O	M	O	M	O	M	O	M	O	M	O	M	O	M	O
Aug 93	0.00598	0.00261	0.0067	0.0057	0	0.0008	0.0007	0.0003	0.0112	0.0052	0.0015	0.006	0	0.0005	0	0.00026	0.02019	0.00915
Nov 93	0	0	0	0.0108	0	0.0084	0	0.0012	0	0.0227	0	0.0108	0	0	0	0	0	0.02988
Feb 94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00044	0
Mar 94	0	0	0.0001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May 94	0	0	0	0	0	0	0.0009	0	0	0	0	0	0.0009	0	0	0	0.00085	0
Aug 94	0	0	0.0032	0	0.0061	0	0.0011	0	0	0	0	0	0	0	0.0004	0	0.00072	0
Sep 94	0	0	0.0019	0	0.0075	0	0	0	0.0006	0	0	0	0	0	0	0	0	0
Nov 94	0.00029	0	0.0021	0	0.0012	0	0.0009	0	0.0026	0	0.0035	0	0	0	0	0	0.04311	0
Dec 94	0	0	0	0	0	0	0	0	0.0015	0	0	0	0	0	0	0	0	0
Jan 95	0	0	0.0033	0.0015	0	0	0.0008	0.0007	0.0016	0.0007	0	0	0	0	0	0	0.00163	0.00524
Feb 95	0	0	0	0.0096	0	0.0014	0	0.0014	0	0	0	0	0	0	0	0	0	0
Mar 95	0	0	0.0027	0.0007	0	0	0	0	0	0	0	0	0	0	0	0	0.00274	0.00068
Apr 95	0	0.00153	0	0	0	0	0	0	0	0.0023	0	0	0	0	0	0	0.038	0.00917
Jun 95	0.00608	0.00159	0	0.0032	0	0	0	0	0	0	0	0	0	0	0	0.00159	0	0.00159
Jul 95	0	0.01503	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aug 95	0.00425	0.01628	0	0.0014	0.0021	0.0007	0	0	0	0.0064	0.017	0.1147	0	0	0	0.00071	0	0.00425
Oct 95	0	0	0	0.0013	0	0	0	0.002	0		0	0.1172	0	0.0293	0	0.00195	0	0.04036
Nov 95	0	0	0.012	0.005	0	0	0	0	0	0	0.004	0.0025	0	0	0	0	0	0.00125
Jan 96	0	0	0.0016	0.0016	0	0	0.0048	0.0024	0	0	0	0	0	0	0	0	0	0
Feb 96	0	0	0	0	0	0	0	0	0.006	0.0043	0	0	0	0	0	0	0	0
Mar 96	0	0	0	0	0	0	0	0	0.0029	0.0011	0	0	0	0	0	0	0	0
Apr 96	0.00161	0.00138	0	0	0	0	0	0	0.0088	0.0115	0.0032	0.0073	0.0113	0.0078	0.0064	0.00826	0.01045	0.01331
May 96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul 96	0	0.00097	0.0019	0.0019	0	0.001	0	0	0	0.001	0	0	0.0014	0.0007	0	0	0	0
Oct 96	0	0	0.0028	0.003	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 14 continued.

	A. pectoralis		*H. capensis*		*L. v. reynaudii*	
	M	G	M	G	M	G
Aug 93	0	0	0	0.0010453	0	0.0018293
Nov 93	0	0.0119509	0	0	0	0
Feb 94	0.0004	0	0.000442	0	0	0
Mar 94	0	0	0	0	0	0
May 94	0	0	0	0	0	0
Aug 94	0.0004	0	0	0	0	0
Sep 94	0.0012	0	0.0018686	0	0	0
Nov 94	0.024	0	0	0	0	0
Dec 94	0	0	0.0007256	0	0	0
Jan 95	0	0	0	0	0	0
Feb 95	0	0	0	0	0	0
Mar 95	0	0	0	0	0	0
Apr 95	0.0173	0.00382	0	0	0	0
Jun 95	0	0	0	0	0	0
Jul 95	0	0	0	0	0	0
Aug 95	0	0.0021237	0	0	0	0
Oct 95	0	0.0013019	0	0.0013019	0	0.0078114
Nov 95	0	0.0031171	0	0.0012469	0	0
Jan 96	0	0	0	0	0	0
Feb 96	0.006	0.0018249	0.0019952	0.0012166	0	0
Mar 96	0	0	0	0	0	0
Apr 96	0.0056	0.007801	0.0016081	0.0013767	0.0024122	0.0032122
May 96	0	0	0	0	0	0
Jul 96	0	0	0	0	0	0
Oct 96	0	0	0	0	0	0

Appendix 15 - Mean size, standard deviation, size range (BL - mm), and number (in parentheses) of fish larvae for each month from all stations sampled during the period August 1993 to October 1996 (* catch comprised a single specimen).

	E. japonicus	*E. whiteheadi*	*S. sagax*	*G. capensis*	*M. capensis*	*L. hectoris*	Gobiesocidae Sp1	Gobiesocidae Sp2
Aug 93	6.17±1.85/10.2-4.0(20)	8.6±1.49/13.7-5.8(208)	7.32±2.24/20.2-3.0(4895)	2.32±0.84/4.5-1.4(33)	2.25±0.43/3.2-1.7(26)		3.52±0.53/5.6-2.6(175)	4.13±0.38/4.6-3.3(16)
Nov 93	7.14±2.2/11.2-3.8(17)	12.61±2.83/17.35-7.5(27)	11.26±1.23/13.2-9.7(10)				3.44±0.74/4.02-2.6(3)	
Feb 94								
Mar 94	20.83±9.41/31.86-7.4(5)	13.98±2.43/17.37-11.38(5)			5.1*			
May 94	2.83±0.62/5.2-2.1(27)		9.9*	1.3*				
Aug 94	5.75*	13.74±2.51/16.51-8.64(12)	11.84±2.76/18.66-6.52(51)	4.51±1.54/5.6-3.42(2)			4.35±0.93/5.2-3.4(4)	4.9*
Sep 94		14.4±9.33/21.0-7.8(2)	9.42±2.58/15.1-6.4(12)	3.5*				
Nov 94	7.72±1.84/3.23-3.0(194)	9.27±4.72/16.0-5.0(7)	7.22±2.15/13.16-2.81(75)		4.2±1.93/6.8-2.2(7)		3.13*	
Dec 94	9.1±0.26/9.3-8.8(3)		9.1*					
Jan 95	4.48±1.56/11.9-1.8(359)							
Feb 95			5.50±0.79/5.7-4.0(4)					
Mar 95								
Apr 95	12.27±3.18/14.3-8.6(3)		16.36±2.54/18.9-12.3(5)	3.9*		6.1*		
Jun 95	5.15±0.49/5.5-4.8(2)	8.54±1.91/10.4-5.9(5)	6.23±0.85/7.7-4.3(16)	4.1*		5.4±0.85/6.0-4.8(2)		
Jul 95	11.81*		11.15±3.36/17.05-4.0(114)	2.81±0.37/3.6-2.2(20)		5.9±0.96/9.0-4.7(22)		
Aug 95		15.3*	8.49±4.44/22.4-2.6(161)	2.63±0.51/3.5-2.1(11)	2.7*	6.35±0.48/6.8-5.8(4)		
Oct 95	7.9±5.43/14.9-2.5(5)	10.77±3.77/17.0-3.0(46)	7.03±3.58/19.4-2.0(174)	7.59±6.63/12.27-2,9(2)	2.74±0.79/4.0-1.8(15)	4.35±0.92/5.0-3.7(2)	4.38±1.01/5.2-2.9(4)	6.8*
Nov 95	5.68±1.78/8.6-4.2(5)	8.4*	6.25±2.08/9.0-4.0(4)					
Jan 96	3.61±1.85/9.6-2.3(18)		10.35±2.54/14.0-8.1(4)					
Feb 96	10.12±1.14/11.7-8.5(6)	13.5*	4.75±0.645.2-4.3(2)		3.9*			
Mar 96	8.48±7.21/19.6-3.2(6)		5.66±2.42/11.0-3.2(9)	21.4*		8.1*		
Apr 96	15.2±2.9/19.3-11.6(5)	13.56±3.08/19.6-7.6(67)			5.13±3.71/5.7-1.9(20)			6.55±0.78/7.1-6.0(2)
May 96				2.1*				
Jul 96	7.1±1.25/8.1-5.7(3)		13.39±2.8/19.7-8.4(32)	3.2±0.28/3.4-3.0(2)	1.6*	6.4*		
Oct 96	5.04±1.86/6.8-2.4(5)		8.97±7.97/17.9-2.6(3)					

Appendix 15 continued.

	C. gymnoderma	*C. capensis*	*P. olivaceum*	*A. argyrozona*	*D. s. capensis*	*C. laticeps*	*P. b. natalensis*	*S. emarginatum*	Sparidae Sp11
Aug 93		3.69±0.83/5.2-2.4(9)	6.3±0.71/7.3-5.4(7)	2.87±0.55/4.5-1.8(102)	2.85±0.48/4.3-1.8(80)	3.08±0.36/3.8-2.6(12)	5.75±0.97/6.8-4.5(2)		3.2*
Nov 93	4.21±1.27/5.35-2.2(6)	3.25*		3.85±0.21/4.0-3.7(2)		3.55*		4.37±0.57/4.86-3.75(3)	
Feb 94									
Mar 94	3.35±0.44/4.1-2.82(6)								
May 94		2.0*							
Aug 94	4.6*		5.9*	4.4*	3.25±0.64/3.7-2.8(2)				
Sep 94				4.8*	2.85±0.21/3.0-2.7(2)				4.6*
Nov 94	4.52±0.73/5.35-3.5(5)					2.8*		4.92±1.55/6.6-2.4(5)	
Dec 94									
Jan 95		4.13±0.75/5.0-3.7(3)					3.6±0.1/3.7-3.5(2)		2.8*
Feb 95	4.6*								
Mar 95									
Apr 95				4.0*					5.3±0.66/6.1-4.5(4)
Jun 95				3.13±0.25/3.4-2.9(3)	7.4*		8.6*		
Jul 95		5.02±0.71/6.25-3.8(25)	6.33±2.37/8.3-3.7(3)		3.66±0.24/3.9-3.0(16)		5.88±2.35/9.12-5.3(3)		3.69±0.43/6.0-2.6(322)
Aug 95	4.7±1.56/5.8-3.6(2)	5.69±1.51/9.4-3.5(35)	5.62±3.06/9.4-2.5(6)	3.87±0.32/4.1-3.5(3)	3.69±0.56/5.0-2.6(12)	6.5*	6.18±0.45/6.6-5.6(7)		5.27±0.84/5.8-4.3(3)
Oct 95	3.0*	3.2±1.36/6.4-1.8(14)							
Nov 95		3.2±0.28/3.4-3.0(2)		3.05±0.21/3.2-2.9(2)		3.93±0.63/4.8-3.3(4)		4.82±1.33/7.6-3.3(12)	
Jan 96				3.3±0/3.3-3.3(2)			4.1*		
Feb 96		3.0*							
Mar 96	4.8*	8.3±1.01/9.4-7.4(3)	5.2±1.69/6.4-4.0(2)	4.5*	4.3*	7.8*	5.46±0.25/5.8-5.1(4)		
Apr 96		3.6*							
May 96	4.83±0.55/5.4-4.3(3)								
Jul 96		5.25±0.35/5.5-5.0(2)	6.1*	3.3*	3.6±0.95/4.7-3.0(3)		4.5*		4.0*
Oct 96	3.0*					5.45±0.21/5.6-5.3(2)			

Appendix 15 continued.

	T. trachurus	Chelidactylidae Sp1	*P. plicornis*	Blenniidae Sp4	Blenniidae Sp5	*P. costatus*	Gobiidae Sp1	Gobiidae Sp2	Gobiidae Sp3
Aug 93	3.0±0.52/5.3-1.7(1588)	3.22±0.64/4.3-2.3(10)	3.39±1.19/6.6-1.9(22)	5.2±0.99/5.9-4.5(2)	3.4*	1.73±0.55/3.0-1.1(20)	3.15±0.71/4.4-2.1(23)	4.05±1.34/5.0-3.1(2)	6.4*
Nov 93			5.71±2.83/10.4-2.8(7)			2.38±1.44/6.25-1.38(11)	4.1±0.65/4.7-3.4(9)		
Feb 94									
Mar 94			3.4*						
May 94					2.5*			1.9*	
Aug 94			4.98±1.18/7.1-3.35(9)	5.32±0.73/6.7-4.4(17)	3.26±0.44/3.7-2.82(3)				11.64*
Sep 94			4.23±1.12/5.5-3.4(3)	5.98±0.93/8.2-5.0(12)		2.4*			
Nov 94	2.5*	34.62*	3.81±1.13/5.5-3.0(7)	4.39±0.63/5.1-3.62(4)	2.23±0.23/2.5-2.1(3)	2.67±0.67/3.42-1.71(9)	2.16±0.24/2.65-1.7(12)		
Dec 94						4.15±2.76/6.1-2.2(2)			
Jan 95			3.88±0.39/4.3-3.5(4)		4.0±1.84/5.3-2.7(2)	2.95±0.78/3.5-2.4(2)			
Feb 95			4.67±0.91/6.3-3.7(7)	5.6*	3.3*				
Mar 95			4.0*						
Apr 95		3.2±0.14/3.3-3.1(2)				2.63±0.29/2.8-2.3(3)			
Jun 95	3.23±0.21/3.4-3.0(3)		4.35±0.49/4.7-4.0(2)						3.7*
Jul 95	4.11±0.65/5.5-3.0(54)	4.06±0.58/5.8-3.3(26)							
Aug 95	4.81±2.14/10.5-2.7(26)	3.76±1.05/6.3-2.6(23)	6.6±1.27/7.5-5.7(2)	8.5*		3.86±1.48/6.3-2.1(9)	5.75±0.95/6.8-4.9(4)		6.1*
Oct 95	3.80±1.19/7.5-2.2(84)		5.25±0.78/5.8-4.7(2)		3.0±0.61/3.4-2.3(3)	1.84±0.81/11.0-1.1(267)	3.5±1.02/5.7-2.2(22)	2.54±0.62/4.5-1.3(49)	7.8±0.46/8.3-7.4(3)
Nov 95	5.4±3.25/7.7-3.1(2)		5.25±1.82/8.3-3.6(8)				4.55±2.47/6.3-2.8(2)		
Jan 96			5.0±0.57/5.4-4.6(2)		3.7±0.53/4.3-3.3(3)				
Feb 96						3.39±1.51/6.6-2.1(7)			
Mar 96	7.85±1.91/9.2-6.5(2)					3.25±1.34/4.2-2.3(2)			
Apr 96		2.77±0.89/3.8-2.2(3)				11.58±4.17/16.2-2.3(20)	4.44±1.37/6.2-1.9(16)	2.35±0.64/4.2-1.3(15)	4.37±1.86/7.6-1.4(16)
May 96									
Jul 96		4.5*	7.2±2.26/8.8-5.6(2)	5.5*		2.2*		4.3*	
Oct 96			6.07±0.21/6.3-5.9(3)						

Appendix 15 continued

	C. zanzibarensis	*A. pectoralis*	*H. cayensis*	*L. v. reynaudii*
Aug 93	3.82±1.55/10.2-1.9(34)		2.75±0.86/4.0-2.1(4)	
Nov 93	5.17±2.28/9.5-2.6(16)	4.76±2.12/7.3-2.8(6)		
Feb 94	1.8*	3.4*	2.2*	
Mar 94				
May 94	3.2*			
Aug 94	4.88±0.75/5.5-4.05(3)	3.26±0.06/3.3-3.21(2)		
Sep 94		3.35±1.34/4.3-2.4(2)	2.73±0.45/3.2-2.3(3)	
Nov 94	4.07±1.32/10.06-1.3(147)	2.69±0.8/5.4-1.6(72)		
Dec 94			6.2*	
Jan 95	4.98±1.83/9.5-2.8(16)			
Feb 95				
Mar 95	4.0*			
Apr 95	6.32±2.13/10.1-3.9(12)	4.36±0.55/5.2-3.8(5)		
Jun 95	5.5*			
Jul 95				
Aug 95	9.07±4.16/17.0-4.8(6)	3.8±1.05/4.8-2.7(3)		
Oct 95	4.47±2.37/14.3-2.0(65)	2.45±0.21/2.6-2.3(2)	1.7±0.28/1.9-1.5(2)	2.03±0.67/3.3-1.5(12)
Nov 95	4.5±0.71/5.0-4.0(2)	2.9±0.51/3.7-2.4(5)	2.8±0.14/2.9-2.7(2)	
Jan 96				
Feb 96		2.83±0.25/3.1-2.6(3)	2.4±0.42/2.7-2.1(2)	
Mar 96				
Apr 96	7.04±3.93/16.3-1.5(25)	3.42±0.64/4.5-2.2(12)	4.13±2.04/5.6-1.8(3)	2.38±0.78/3.4-1.1(7)
May 96				
Jul 96				
Oct 96				

Appendix 16 - Species of fish recorded in the Tsitsikamma National Park, either as adults, juveniles or larvae. Habitat is that of adult fish with E - Estuary, I - Intertidal, SR - Subtidal Reef, S - Subtidal over soft sediments, P - Pelagic. Source references are as follows, 1 - Buxton & Smale (1984), 2 - Burger (1990), 3 - Tilney & Buxton (1994), 4 - This study, 5&6 - fish caught during offshore and rock & surf based tagging projects in the Tsitsikamma respectively, 7 - Diving Observations. The symbol * denotes a species endemic to Southern Africa according to Smith & Heemstra (1986).

ORDER & FAMILY	SPECIES	SMITH'S #	COMMON NAME	ADULT HABITAT	SOURCE REFERENCE
Order Hexanchiformes					
Hexanchidae	*Notorynchus capedianus*	2.4	Broadnose sevengill shark	S, SR, P	5, 7
Order Squaliformes					
Squalidae	*Squalus megalops*	5.26	Bluntnose spiny dogfish	SR, S	5
Order Carcharhiniformes					
Carcharhinidae	*Carcharhinus brachyurus*	9.5	Copper shark	SR, P	2, 5, 6, 7
	Carcharhinus brevipinna	9.6	Spinner shark	P	5
	Carcharhinus obscurus	9.14	Dusky shark	S, SR, P	5
	Galeorhinus galeus	9.20	Soupfin shark	S, SR, P	2, 5, 6
	Mustelus mustelus	9.27	Smooth-hound	S, SR, P	2, 5, 6
	*Mustelus palumbes**	9.28	Whitespotted smooth-hound	S, SR, P	5
	Prionace glauca	9.32	Blue shark	P	5, 7
	*Triakus megalopterus**	9.36	Spotted gullyshark	SR	2, 5, 6
Scyliorhinidae	*Halaelurus natalensis**	11.7	Tiger catshark	SR	5
	*Haploblepharus edwardsii**	11.8	Puffadder shyshark	SR	2, 5, 6
	*Haploblepharus fuscus**	11.9	Brown shyshark	SR	2, 5, 6
	*Haploblepharus pictus**	11.10	Dark shyshark	SR	2
	*Poroderma africanum**	11.13	Striped catshark	SR	1, 2, 5, 6
	*Poroderma pantherinum**	11.15	Leopard catshark	SR	1, 2, 5, 6
	*Scyliorhinus capensis**	11.16	Yellowspotted catshark	SR	5, 6
Sphyrnidae	*Sphyrna zygaena*	13.3	Smooth hammerhead	P	2, 5
Order Lamniformes					
Lamnidae	*Carcharodon carcharias*	14.1	Great white shark	P	2
Odontaspididae	*Eugomphodus taurus*	19.1	Spotted ragged-tooth	SR	1, 2, 5
Order Torpediniformes					
Torpedinidae	*Torpedo fuscomaculata*	23.1	Blackspotted electric ray	SR	2
Order Rajiformes					
Rhinobatidae	*Rhinobatos annulatus**	27.2	Lesser guitarfish	SR, S	2, 6
Order Myliobatiformes					
Myliobatidae	*Myliobatis aquila*	28.2	Eagleray	SR	2
	Pteromylaeus bovinus	28.3	Bullray	SR	7
Dasyatidae	*Dasyatis pastinaca*	30.3	Blue stingray	SR, S	7
	*Gymnura natalensis**	30.7	Backwater butterflyray	SR	2
Order Anguilliformes					
Congridae	*Conger wilsoni*	40.8	Cape conger	I, SR	1, 2
Order Clupeiformes					
Clupeidae	*Etrumeus whiteheadi**	54.2	Redeye roundherring	P	3, 4
	Sardinops sagax	54.12	South African pilchard	P	3, 4
Engraulidae	*Engraulis japonicus*	55.1	Cape anchovy	P	3, 4
Order Gonorhynchiformes					
Gonorhynchidae	*Gonorhynchus gonorhynchus*	57.1	Beaked sandfish	S, P	4

Appendix 16 continued.

ORDER & FAMILY	SPECIES	SMITH'S #	COMMON NAME	ADULT HABITAT	SOURCE REFERENCE
Order Siluriformes					
Ariidae	*Galeichthys ater**	59.2	Black seacatfish	SR. S	2
	*Galeichthys feliceps**	59.3	White seacatfish	SR. S	1. 2
Plotosidae	*Plotosus nkunga*	60.2	Eel-catfish	I. SR	7
Order Myctophiformes					
Myctophidae	*Diogenichthys atlanticus*	86.42	Laternfish	P	4
	Lampanyctodes hectoris	86.72	Onderbaadjie	P	4
	Symbolophorus barnardi	86.119	Laternfish	P	4
Order Gadiformes					
Gadidae	*Gaidropsarus capensis**	88.1	Cape rockling	I. SR	1. 2. 3. 4
Merlucciidae	*Merluccius capensis*	89.4	Shallow-water hake	S	4. 5
Moridae	*Physiculus capensis**	90.7	Deepsea cod	SR. S. P	4
Bregmacerotidae	*Bregmaceros atlanticus*	92.1	Codlet	SR. S	4
Order Ophidiiformes					
Ophidiidae	*Genypterus capensis**	96.9	Kingklip	S	4
Bythitidae	*Bidenichthys capensis**	98.1	Freetail brotula	I. SR	1. 2
	Dermatopsoides talboti	98.6	Lesser orange brotula	S	2
	*Grammonoides opisthodon**	98.8	Bighead brotula	S	2
Order Batrachoidiformes					
Batrachoididae	*Batrichthys apaiatus**	100.3	Snakehead toadfish	I. SR	2
	*Chatrabus hendersoni**	100.5	Chocolate toadfish	I. SR	2
	*Chatrabus melanurus**	100.6	Humpback toadfish	SR	1
Order Lophiiformes					
Lophiidae	*Lophius upsicephalus**	101.4	Monk	S	4
Order Gobiesociformes					
Gobiesocidae	*Apletodon pelegrini*	110.1	Chubby clingfish	I. SR	2
	*Chorisochismus dentex**	110.2	Rocksucker	I. SR	2
	*Diplecogaster megalops**	110.3	Bigeye clingfish	I. SR	1
Order Beryciformes					
Berycidae	*Centroberyx spinosus**	126.3	Short alfonsino	SR	1. 2
Order Syngnathiformes					
Syngnathidae	*Syngnathus acus*	145.29	Longsnout pipefish	E. SR. P	2. 3. 4
Order Scorpaeniformes					
Tetrarogidae	*Coccotropsis gymnoderma**	150.2	Smoothskin scorpionfish	SR	1. 2. 3. 4
Congiopodidae	*Congiopodus spinifer**	152.1	Spinenose horsefish	SR	3. 4
	*Congiopodus torvus**	152.2	Smooth horsefish	SR	7
Triglidae	*Chelidonichthys capensis**	157.1	Cape gurnard	SR. S	3. 4
	Chelidonichthys kumu	157.2	Bluefin gurnard	SR. S	7
	*Trigloporus lastoviza africanus**	157.7	African gurnard	SR. S	1
Order Perciformes					
Kuhliidae	*Kuhlia mugil*	164.1	Barred flagtail	I. SR. S	2
Serranidae	*Acanthistius sebastoides**	166.1	Koester	SR	1. 2
	Anthias squamipinis	166.9	Sea goldie	SR	7
	*Epinephelus andersoni**	166.34	Catface rockcod	SR	7
	Epinephelus emarginata	166.43	Yellowbelly rockcod	I. SR	1. 2. 5. 6
	Serranus cabrilla	166.76	Comber	SR	2. 4
Teraponidae	*Terapon jarbua*	173.2	Thornfish	E. SR	7

Appendix 16 continued.

ORDER & FAMILY	SPECIES	SMITH'S #	COMMON NAME	ADULT HABITAT	SOURCE REFERENCE
Scombropidae	*Scombrops boops**	176.6	Gnomefish	SR. S	1. 2
Pomatomidae	*Pomatomus saltatrix*	178.1	Elf	E. SR. S	1. 5. 6
Haemulidae	*Pomadasys commersonnii*	179.10	Spotted grunter	E. SR. S	1. 6
	Pomadasys olivaceum	179.17	Piggy	E. SR	1. 2. 3. 4. 5. 6
	Pomadasys striatum	179.18	Striped grunter	SR	1. 2
Sparidae	*Argyrozona argyrozona**	183.5	Carpenter	SR	1. 2. 4. 5
	*Boopsoidea inornata**	183.6	Fransmadam	SR	1. 2. 4. 5. 6
	Cheimerius nufar	183.7	Santer	SR	2. 6
	*Chrysoblephus cristiceps**	183.9	Dageraad	SR	1. 2. 5
	*Chrysoblephus gibbiceps**	183.10	Red stumpnose	SR	1. 2. 5
	*Chrysoblephus laticeps**	183.11	Roman	SR	1. 2. 4. 5. 6
	*Cymatoceps nasutus**	183.15	Black musselcracker	SR	1. 2. 5. 6
	*Diplodus cervinus hottentotus**	183.16	Zebra	E. I. SR	1. 2. 3. 4. 6
	Diplodus sargus capensis	183.17	Blacktail	E. I. SR	1. 2. 3. 4. 6
	*Gymnocrotaphus curvidens**	183.18	Janbruin	I. SR	1. 2. 6
	*Lithognathus lithognathus**	183.2	White steenbras	E. SR. S	1. 2. 6
	Lithognathus mormyrus	183.21	Sand steenbras	E. SR. S	1. 2. 6
	*Pachymetopon aneum**	183.22	Blue hottentot	SR	1. 2. 5. 6
	*Pachymetopon blochii**	183.23	Hottentot	SR	5
	Pachymetopon grande	183.24	Bronze bream	SR	1. 2. 6
	Pagellus bellottii natalensis	183.25	Red tjor-tjor	SR. S	1. 3. 4. 5
	*Petrus rupestris**	183.26	Red steenbras	SR	1. 2. 5. 6
	*Polysteganus undulosus**	183.32	Seventy-four	SR	7
	*Porcostoma dentata**	183.33	Dane	SR	1
	*Pterogymnus laniarius**	183.34	Panga	SR	1. 5
	*Rhabdosargus globiceps**	183.35	White stumpnose	SR	1. 2
	*Rhabdosargus holubi**	183.36	Cape stumpnose	E. I. SR	1. 2. 6
	Sarpa salpa	183.39	Strepie	E. I. SR	1. 2. 4. 6
	*Sparodon durbanensis**	183.40	White musselcracker	I. SR	1. 2. 6
	*Spondyliosoma emarginatum**	183.41	Steentjie	SR	1. 2. 3. 4. 5. 6
Centracanthidae	*Spicara axillaris**	184.2	Windtoy	SR. S	2
Dichistidae	*Dichistius capensis**	187.1	Galjoen	SR	1. 2. 6
	Dichistius multifasciatus	187.2	Banded galjoen	SR	2. 6
Parascorpididae	*Parascorpis typus**	188.1	Jutjaw	SR	2
Scorpididae	*Neoscorpis lithophilus**	190.1	Stonebream	SR	2. 6
Monodactylidae	*Monodactylus falciformis*	193.2	Cape moony	E. SR	1. 2. 3. 4
Mullidae	*Parupeneus rubescens*	196.10	Blacksaddle goatfish	SR	1. 2
Sciaenidae	*Argyrosomus innodorus*	199.1a	Silver kob	E. SR. S	1. 5
	Argyrosomus japonicus	199.1b	Dusky kob	E. SR. S	2. 6
	Atractoscion aequidens	199.3	Geelbek	SR. S. P	1. 3. 4
	Umbrina canariensis	199.8	Baardman	SR	2
	Umbrina ronchus	199.9	Slender baardman	SR	7
Pomacanthidae	*Pomacanthus rhomboides*	204.12	Old woman	SR	7
Chaetodontidae	*Chaetodon blackburnii*	205.3	Brownburnie	SR	7
	*Chaetodon marleyi**	205.11	Doublesash butterflyfish	SR	1. 2
	Heniochus acuminatus	205.22	Coachman	SR	7

Appendix 16 continued.

ORDER & FAMILY	SPECIES	SMITH'S #	COMMON NAME	ADULT HABITAT	SOURCE REFERENCE
Oplegnathidae	*Oplegnathus conwayi**	206.1	Cape knifejaw	SR	1, 2
	*Oplegnathus robinsoni**	206.3	Natal knifejaw	SR	7
Carangidae	*Lichia amia*	210.33	Garrick	E, SR, P	2
	Seriola lalandi	210.44	Giant yellowtail	SR, P	1, 2, 4
	Trachurus trachurus	210.52	Maasbanker	SR, P	2, 3, 4
Cheilodactylidae	*Cheilodactylus fasciatus**	215.1	Redfingers	I, SR	1, 2, 3, 4
	*Cheilodactylus pixi**	215.2	Barred fingerfin	SR	1, 2
	*Chirodactylus brachydactylus**	215.3	Twotone fingerfin	I, SR	1, 2, 4
	*Chirodactylus grandis**	215.4	Bank steenbras	SR	1, 2
Pomacentridae	*Abudefduf sordidus*	219.5	Spot damsel	SR	7
	*Chromis dasygenys**	219.13	Bluespotted chromis	SR	7
Labridae	*Coris caudimacula*	220.21	Spottail coris	SR	7
	Labroides dimidiatus	220.41	Bluestreak cleaner wrasse	SR	7
Mugilidae	*Liza richardsonii**	222.7	Southern mullet	E, I, S, P	2, 4
	Mugil cephalus	222.10	Flathead mullet	E, S, P	4
Congrogadidae	*Halidesmus scapularis**	227.1	Snakelet	I, SR	1, 2
Champsodontidae	*Champsodon capensis*	229.1	Gaper	P	4
Blenniidae	*Chalaroderma ocellata**	235.7	Two-eyed blenny	I, SR	1, 2
	*Parablennius cornutus**	235.31	Horned blenny	I, SR	2
	Parablennius pilicornis	235.33	Ringneck blenny	I, SR	1, 2, 3, 4
	Plagiotremus rhinorhynchos	235.37	Twostripe blenny	SR	7
	Plagiotremus tapeinosoma	235.38	Piano blenny	SR	2
	Scartella emarginata	235.40	Maned blenny	SR	4
	Xiphasia setifer	235.42	Snakeblenny	SR	7
Tripterygiidae	*Cremnochorites capensis**	236.1	Cape triplefin	SR	2
Clinidae	*Blennioclinus brachycephalus**	237.1	Lace klipfish	I	1, 2
	*Blennioclinus stella**	237.2	Silverbubble klipfish	SR	2
	*Blennophis striatus**	237.4	Striped klipfish	I, SR	1, 2
	*Cirrhibarbis capensis**	237.7	Barbelled klipfish	I,SR	2
	*Climacoporus navalis**	237.8	Fleet klipfish	I, SR	2
	*Clinus acuminatus**	237.10	Sad klipfish	I, SR	2
	*Clinus agilis**	237.11	Agile klipfish	E, I	2
	*Clinus berrisfordi**	237.12	Onrust klipfish	SR	2
	*Clinus cottoides**	237.14	Bluntnose klipfish	I, SR	2
	*Clinus nematopterus**	237.18	Chinese klipfish	SR	2
	*Clinus robustus**	237.19	Robust klipfish	SR	2
	*Clinus superciliosus**	237.22	Super klipfish	I, SR	2
	*Clinus taurus**	237.23	Bull klipfish	SR	2
	*Clinus venustris**	237.24	Speckled klipfish	I, SR	2
	*Pavoclinus graminis**	237.28	Grass klipfish	I, SR	2
	*Pavoclinus laurentii**	237.30	Rippled klipfish	I, SR	1
	*Pavoclinus pavo**	237.34	Peacock klipfish	I, SR	1, 2
	*Pavoclinus profundus**	237.35	Deepwater klipfish	SR	1, 2
	*Xenopoclinus kochi**	237.37	Platanna klipfish	I, SR	2
	*Xenopoclinus leprosus**	237.38	Leprous platanna klipfish	I, S	1, 2
Ammodytidae	*Gymnammodytes capensis**	238.2	Cape sandlance	S	3, 4

Appendix 16 continued.

ORDER & FAMILY	SPECIES	SMITH'S #	COMMON NAME	ADULT HABITAT	SOURCE REFERENCE
Callionymidae	*Paracallionymus costatus**	239.6	Ladder dragonet	SR, S	3, 4
Gobiidae	*Caffrogobius agulhensis**	240.19	Agulhas goby	SR	1, 2
	*Caffrogobius caffer**	240.20	Banded goby	I, SR	2
	*Caffrogobius saldanha**	240.24	Commafin goby	SR	2
Zanclidae	*Zanclus canescens*	244.1	Moorish idol	SR	2
Gempylidae	*Thyrsites atun*	247.8	Snoek	P	4
Trichiuridae	*Lepidopus caudatus*	248.4	Buttersnoek	S, P	4
Scombridae	*Scomber japonicus*	249.11	Mackerel	S, SR, P	4, 5, 7
Order Pleuronectiformes					
Bothidae	*Arnoglossus capensis**	259.1	Cape flounder	S	4
Cynoglossidae	*Cynoglossus capensis**	261.3	Sand tonguefish	S	3, 4
	Cynoglossus zanzibarensis	261.9	Redspotted tonguefish	S	3, 4
Soleidae	*Austroglossus pectoralis**	262.3	East coast sole	S	4
	*Heteromycteris capensis**	262.5	Cape sole	E, S	3, 4
	Monochirus ocellatus	262.7	Foureye sole	S	4
	*Solea bleekeri**	262.12	Blackhand sole	E, S	3, 4
	*Solea fulvomarginata**	262.13	Lemon sole	S	2
	Synaptura marginata	262.14	Shallow-water sole	E, S	3
	Synapturichthys kleini	262.15	Lace sole	S	4
Order Tetraodontiformes					
Tetraodontidae	*Amblyrhynchotes honckenii*	268.1	Evileye blaasop	SR	2, 3
Molidae	*Mola mola*	270.2	Ocean sunfish	P	2