T ASPECTS OF THE BIOLOGY AND ECOLOGY
OF THE ESTUARINE FISHES OF THE
EAST COAST OF SOUTH AFRICA

SR by

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1. INTRODUCTION

The East Coast of South Africa supports an extremely diverse fish fauna which has been studied taxonomically in considerable detail but remarkably little in terms of its biology and ecology. The need for this type of research has developed progressively during the past 30 years due to the decline in availability of certain species in response to factors such as commercial line fishing, sport angling, spearfishing and environmental degradation. Furthermore, concern over the state of the fauna and the lack of research has been stimulated by an increasing awareness that it constitutes a valuable national asset. Not only does it contribute substantially towards the multi-million Rand real estate and tourist industry on the coast, but its recreational and food production potential are assuming greater importance as human population density increases.

Consideration of these factors led the Oceanographic Research Institute to undertake biological and ecological research on teleost fishes. In view of the diversity of the fauna and of its environment, great care had to be taken to set research priorities so as to investigate the most serious problems first. It was decided that priority should be given to fishes living in endangered and degraded habitats rather than to individual species subject to heavy exploitation. This was based on the conviction that serious long-term and sometimes irremediable damage can result from the former, whereas exploited species have a natural ability to recover if fishing effort is reduced.

Consideration of the various ecological components of the teleost fauna led to the conclusion that the fishes which utilize the estuarine environment for part of their lives were most urgently in need of study. Although some of these species are of more obvious significance than others, it was deemed advisable not to concentrate on them alone but to adopt a broad approach to the fish fauna as a whole. The main object was to provide the factual information on the biology and ecology of the fauna necessary to assess whether it is threatened by exploitation and environmental degradation.

Research has been financed jointly by the South African National Committee for Oceanographic Research and by the South African Association for Marine Biological Research (the parent body of the Oceanographic Research Institute, Durban). It has been conducted in collaboration with the Branch Sea Fisheries and the Natal Parks Board which are vested with the responsibility for the management and conservation of South Africa's marine and estuarine resources.

Preliminary sampling was started in August 1968 and was followed by five years of intensive research between January 1969 and December 1973. This was concentrated in Natal but also extended north to Mozambique and south into the Cape Province. The estuaries that received most attention were the St. Lucia lake system, Richards Bay and Durban Bay. Sampling of estuarine fish during the marine phase of their life cycles took place along most of the Natal coast but was more intense in the Durban area. The main species included in the programme were the spotted grunter (*Pomadasys commersonni*), Natal stumpnose (*Rhabdosargus sarba*), kob *Argyrosomus hololepidotus*) and the grey mullet (*Mugil cephalus*). Numerous other species were also studied.

It is planned to publish the results in a series of papers and the thesis constitutes the first step in this process. However to prevent it from becoming excessively long its scope has been restricted to certain aspects of the overall programme.

At the start an attempt is made to cast the fish fauna in its ecological setting by describing the main physical features of the environment and some of the factors which influence it. The diversity of the fauna is indicated in a checklist and attention is drawn to the species that were sampled in greatest abundance. Their distribution on the East Coast of South Africa and relationship to the faunas of the tropical Indo-Pacific and Atlantic are described.

The main body of the thesis consists of the presentation and discussion of results under the following headings: Length composition of estuarine and marine populations; Seasonal abundance and migrations; Reproduction; and Recruitment of juveniles into estuaries. Finally, under the heading General Discussion, the results are collated and conclusions are drawn concerning the most salient features of the biology and ecology of this group of fishes. An assessment is made of its degree of dependence on the estuarine environment and on the probable effects of exploitation and environmental degradation.

2. PHYSICAL FEATURES OF THE ENVIRONMENT

The biology and ecology of estuarine fishes is greatly influenced by physical features of the marine, terrestrial and estuarine environments. An outline of their main characteristics is therefore given below.

2.1 Marine Environment

The general features that have been described are drawn from published work by Harris (1961), Oliff (1969), Anderson *et al* (1970), Duncan (1970) and Pearce (1973).

Agulhas Current

The main currents of the south west Indian Ocean are shown in Fig.1. In the north east the westward flowing Equatorial Current divides into two branches which flow southwards as the East Madagascar Current and the Mozambique Current. The former, after rounding the southern tip of Madagascar, flows in a westerly direction until it meets the African coastline at about 25°S. Here it combines with the Mozambique Current to form the strong south west flowing Agulhas Current.

The flow of the Agulhas Current varies seasonally, being stronger in the southern summer when the Somali Current flows southwards along the north east coast of Africa and reinforces the Mozambique Current. During summer and autumn the Agulhas Current penetrates so far south westwards that its influence is felt in False Bay (south of Cape Town, Fig.2) where components of the warm Indian Ocean fish fauna are recorded. During winter the Somali Current reverses its direction and the Equatorial Current moves further north. This reduces the strength of the Mozambique Current which may form a more or less discrete circulation in the Mozambique Channel. Under these circumstances the Agulhas Current is mainly derived from the East Madagascar Current. Current speeds usually vary between 1 and 2m/sec.

The distance from the shore of the western (inner) boundary of the Agulhas Current is variable as it has a sinuous motion, but in general it follows the edge of the continental shelf. Along the Zululand coast this is very narrow and the current is consequently within a few kilometres of the shore. South of Port Durnford the shelf widens to a maximum width of 45 kilometres in the vicinity of the Tugela river and the current is correspondingly far from the coast. To the south it again sweeps closeeeinshoreee end

Inshore currents

The inshore currents of the Natal coast are influenced by the Agulhas Current, the western edge of which generates eddies that are most pronounced where the continental shelf is wide. Most of the water movements are parallel to the shelf break and are characterised by current reversals at fairly regular intervals of one to three days. These reversals are directly related to the atmospheric low pressure systems that move along the coast in a north easterly direction. As these are more pronounced during autumn and winter there tends to be a more clearly defined northgoing component (counter current) at this time of the year. Net movement in a northerly direction has been recorded at a number of localities and was incorporated in the coastal model prepared by Anderson et al (1970) for the Durban area. However it is apparent that conditions vary on different parts of the coast as net southerly movement has been recorded off Richards Bay and Cape St. Lucia.

Temperature

Mean surface temperatures in the Agulhas Current range between 23 - 28°C.

The temperature of the inshore water is somewhat lower than that of the Agulhas Current and ranges from 16 - 26°C. This is associated with upwelling, which in the vicinity of Richards Bay has been shown to result from an onshore tendency near the seabed and an offshore tendency at 10m. At this depth the horizontal temperature picture consists of a series of isotherms parallel to the shelf break. Cooler water may also be transported into the Natal region by the counter current.

Surf zone circulation

In this zone circulation tends to be 'cell-like'. Water is brought in by waves and breakers over a broad front and then moves parallel to the beach (usually due to the oblique approach of the breakers), before returning seaward in a rip current. It then comes under the influence of the inshore coastal current before the cycle starts again. Rip currents flow seaward at intervals of about 600m and the water in each cell is discharged approximately every hour.

Salinity

Studies in the vicinity of Richards Bay (Pearce, 1973) have shown that the salinity of the inshore water is reduced by land runoff but that this is predominantly a surface effect. In the 0-20m depth range winter and spring salinities ranged between 35.3 and 35.35°/oo, while in summer and autumn levels dropped to between 35.05 and 35.21°/oo. Salinity contours were roughly parallel to the shelf break and therefore to the current flow direction. In the immediate vicinity of estuary mouths more marked salinity reductions occur.

Similar characteristics are likely to prevail along much of the Natal coast south of St. Lucia as well as on the Transkei coast due to the many rivers which enter the sea in this region.

Turbidity

Due to the general nature of the terrestrial environment (see below) most East Coast rivers carry heavy silt loads during the summer rainy season. Silt fans often extend kilometres out to sea in the vicinity of river mouths and inshore currents ensure that this turbid water is distributed along the coast. It is only north of St. Lucia on the Zululand coast where there are no rivers that clear water conditions exist.

2.2 Terrestrial environment

Natal is extremely rugged, the Drakensberg mountains attaining an altitude of 3385m within 250km of the coast. According to King (1972) this steep relief has developed through monoclinal tilting of the Province along a hinge located near the present coastline; thus elevating the interior, drowning the coast and continental shelf and imparting a smooth profile to the coastal margin. Eustatic rise in sea level is also considered to have contributed to drowning of the coast (du Toit, 1954).

Due to the steep topography the rivers flow rapidly and transport large quantities of sediment onto the continental shelf. This action is intensified by the high rainfall of 800 - 1000mm (Weather Bureau (1972), WB 35) which falls seasonally causing rivers to flow most strongly from November to March. Man-induced destruction of ground cover has increased this natural sediment transport.

Another effect of the steep topography is the large number of rivers that occur south of St. Lucia on the Natal and Transkeian coasts. North of St. Lucia the frequency of rivers entering the sea drops dramatically due to the flatter topography of the Zululand coastal plain which directs the Mkuze river southwards into St. Lucia lake and the Pongola and other rivers in a northerly direction to finally enter the sea at Delagoa Bay.

2.3 Estuarine environment

In most cases the estuaries formed at the river mouths take the form of narrow lagoons of varying lengths, the only extensive estuarine areas in Natal being Richards Bay, Durban Bay and the St. Lucia and Kosi lake systems. The approximate estuarine areas are as follows :

Estuary	Area (ha)
St. Lucia Lakes	31000
Kosi Lakes	3836
Richards Bay	2987
Durban Bay	1061
Umlalazi	132
Amatikulu	122
29 smaller estuaries	280
TOTAL	39418

It is obvious that St. Lucia is the major estuarine system in Natal and in fact it is by far the largest in South Africa. Details of St. Lucia, Richards Bay and Durban Bay are provided later under Section 3.3.

The frequency of estuaries is extremely high south of St. Lucia, a total of 33 estuaries occurring in the approximately 390km between this point and the boundary of Natal. An even higher frequency occurs further south along the Transkeian coast where there are many beautiful lagoons of between 100 - 150ha in extent, but no extensive lake systems. Although these smaller estuaries do not contribute greatly to the total estuarine area on the East Coast their significance must not be underestimated. By providing a continuous sequence of estuarine environments over a long stretch of coast they assist in the south-westward distribution of sub-tropical organisms. This is likely to be most important in those species where the survival of juvenile stages is partly (or wholly) dependent on migration into the estuarine nursery habitat. Furthermore, as the productivity of estuaries is largely dependent upon aquatic vegetation and as much of this grows along the shallow estuarine margins, small systems with a large perimeter relative to area are likely to be more significant than a superficial assessment based on their area alone is likely to suggest. This is particularly true for those species which are epiphytic feeders and graze algae growing on reed stems, mangrove roots and submerged macrophytes.

A marked discontinuity in the distribution of estuaries occurs north of St. Lucia where the Kosi lakes represent the only estuarine system in the 300km between St. Lucia and Delagoa Bay. This system differs from those further south in that it opens onto a stretch of coast where even in the summer the inshore water is clear and silt free. Another feature is that there is very little siltation in the lakes themselves because their catchment consists of the flat sand country of the Zululand coastal plain. Thus the origin of this system as a drowned river valley (Hill, 1969; King, 1972) is not camouflaged through later infilling by river bourne sediments and the Kosi lakes are consequently much deeper (max. 30m; Hill, 1969) than any of the estuaries to the south where active infilling has occurred. The Kosi lakes are thus the exception; most of Natal's estuaries being shallow systems ranging from 1 - 3m in depth.

Present-day estuarine substrates reveal that deposition of river bourne sediments is still active and in the wider lagoon systems where river velocities become reduced, deposition of the finer fractions gives rise to muddy bottoms. These usually change to sandy/mud bottoms in the lower reaches and finally to the coarse shifting beach sand typically found at the estuary mouths. These marine sands are moved by longshore currents and tend to form bars across estuary mouths during periods of low outflow. There are therefore many small blind lagoons and even the bigger systems tend to have narrow channels linking them with the sea.

Scouring of sandbars usually takes place a few times each rainy season and due to the shallowness of the estuaries causes rapid reductions in water salinity. Hill (1966) reports salinity stratification in the Umlalazi lagoon and surface outflow of fresh water, but this estuary is deeper than most (3m) and it seems unlikely that stratification will persist under conditions of very strong river outflow. In the nearby Amatikulu lagoon Hemens _et al_ (1972) report that when the river was flowing strongly some subsurface intrusion of sea water took place at high tide but that this was no longer evident at low tide. Thus marked reductions in salinity to almost fresh conditions are likely to occur for short periods in many Natal estuaries during the average wet season. Under flood conditions marked reductions to virtually freshwater levels even occur in the big systems such as Richards Bay and St. Lucia.

As far as is known the small blind estuaries experience salinities considerably lower than sea water during the winter months and with the advent of the spring rains salinities drop further in response to fresh water inflow exceeding losses by evaporation and seepage. Hypersalinity seems to be a feature which is only exhibited by the St. Lucia lakes where in dry years the lake level drops below mean sea level and sea water flows into the system. Further evaporation causes an increase above 35°/oo (for details see Section 3.3.1).

The estuaries of Natal and the Transkei range in latitude from 27°S to 32°40'S but are warmer than would be expected due to the effects of the south west flowing Agulhas current. Thus mangroves occur throughout both areas and have their southern limit of distribution close to the Kei river. The estuaries of Natal can be described as sub-tropical, and although there is a gradual reduction in temperature towards the south west, this is probably also true for most Transkei estuaries. Approximately 200km to the south Blaber (1973) describes the Kleinemond estuary (latitude 33° 32'S) as warm temperate, but quite where the transition lies has not been determined.

3. THE PROGRAMME OF RESEARCH

3.1 State of knowledge at the start of the programme

The earliest publications dealing exclusively with the fish fauna of South African seas date back to Smith (1849) and Pappe (1853), but it was only about the turn of the century that ichthyological studies became greatly intensified and numerous publications on the subject became available. A list of these is provided by Smith (1949, p.492), from which it is clear that the major workers were Boulenger (1902-1904), Gilchrist (1902-1924), Regan (1906-1921), Thompson (1914 - 1918), von Bonde (1921-1923), Barnard (1923-1948), Fowler (1925-1935) and Smith (1931-1968). Because of the rich ichthyofauna of the South African region these workers concentrated their efforts on taxonomic studies; research on life histories only being undertaken on the relatively few species of economic value to the fishing industry. In more recent years biological studies have been intensified, the work of Davies (1954-1958) on the pilchard Sardinops ocellata and the maasbanker Trachurus trachurus deserving special mention. However due to the fact that the fishing industry is located on the west and south west coasts, the biology of east coast species has been largely neglected. Published information has been fragmentory and has taken the form of brief comments incidental to taxonomic papers. These have been synthesised by Professor J.L.B. Smith in his monumental work, the Sea Fishes of Southern Africa, which includes notes on geographical distribution, the maximum sizes attained and in some cases observations on the habits of adults and the occurrence of young stages in estuaries. Additional information of this sort is to be found in his papers on the Mugilidae (Smith 1947), Sparidae (Smith 1938) and the spotted grunter Pomadasys commersonni(Smith 1950, 1961).

Despite Smith's endeavours very little was known about the biology of the teleost fauna of South African estuaries until Professor J.H. Day and his co-workers conducted their extensive ecological surveys. The resulting series of papers published during the years 1951 - 1974 provides a valuable review of estuarine conditions from the tropical Morrumbene estuary on the coast of Mozambique, through the sub-tropical and warm-temperate estuaries of the East and South coasts, and around the southern tip of Africa to the temperate estuaries of the Atlantic West Coast. A standard approach was adopted whereby each estuary was described according to its topography, physico-chemical conditions, habitat types, and the ecology and composition of its fauna and flora. As a result the species composition of the estuarine fish fauna became well documented and data on the biology of the more important fish species were collected. Although there was always the intention to publish on the biology of the fishes, this was unfortunately never done. Published information thus takes the form of biological comments of a general nature, as well as some more detailed information on aspects of the biology of fishes in certain specific estuarine systems. In the former category I would place papers on the estuary of the Orange river (Brown, 1959); Milnerton estuary and Diep river, Cape (Millard and Scott, 1954); Klein river estuary, Hermanus, Cape (Scott, Harrison and Macnae, 1952); Knysna estuary (Day, Millard and Harrison, 1952); Richards Bay (Millard and Harrison, 1952); the Kosi Bay estuarine lakes (Broekhuysen and Taylor, 1959); and the Morrumbene estuary (Day, 1974). In the latter category the most informative paper is undoubtedly that on the biology of Durban Bay (Day and Morgans, 1956), followed by two papers on the St. Lucia estuarine lake system (Day, Millard and Broekhuysen, 1954; Millard and Broekhuysen, 1970). Interpretation of the data obtained during these surveys was in some measure aided by the results published by Talbot (1955) who studied the biology of the white stumpnose *Rhabdosargus globiceps*, an endemic species which occurs both in estuaries and at sea. Although common on the West and South coasts of South Africa, it is only occasionally seen in the Natal region.

Surprisingly, in the 14 years which elapsed between the publication of Talbot's paper and the start of the present programme, no new detailed study of the life history of an estuarine fish species was undertaken. A review of the state of knowledge of the biology of estuarine fishes at the start of the present programme has therefore to be based on the literature already quoted above. This reveals that the basic pattern of utilisation of estuaries by fishes was understood in its broadest terms. Breeding was considered to take place at sea, with adult fish moving into estuaries to feed. Juveniles were known to be abundant in the estuarine environment which served a nursery function by providing rich feeding grounds (particularly in areas with prolific aquatic vegetation), as well as protection from predators. A start had been made in the study of feeding habits within certain estuaries and estimates of size at sexual maturity and breeding season had been made for some of the species of major importance (more detailed reference will be made to these data in the relevant sections of this thesis). However it was only in the case of R. globiceps that comprehensive data on growth rate, ageing, feeding, length frequency composition and size at maturity were available, and for which sampling in the estuarine and marine environments had proved conclusively that spawning occurred at sea and that only the juvenile phase was represented in estuaries.

Thus at the start of the present programme broad guidelines to the biology of estuarine fish were available in the literature. However there was a great need for factual documentation of biological events for which little or no evidence was available and for a detailed exploration of the biology and ecology of the estuarine teleost fauna of Natal in both its estuarine and marine phases.

3.2 Outline of sampling programme

Due to the wide scope of the programme it was necessary to divide it into the following phases:

Feasibility study: August to December 1968
Biology of adult fish in estuarine environment: 1969 and 1970
Biology of juvenile fish in estuarine environment: 1971
Biology of adult fish in marine environment: 1972
Aspects arising from previous phases, including the geographic distribution of juveniles in estuaries: 1973

At the outset it was intended to concentrate most research effort on the St. Lucia Lake system as this is Natal's largest and richest estuarine area and is, furthermore, administered as a wildlife sanctuary. Thus it would be possible to apply the results more directly for purposes of conservation than in other estuarine systems which fulfil multiple functions. It was considered reasonable to suppose that the results obtained at St. Lucia would be generally applicable to estuarine fish in Natal, so diversification of the programme to include intensive sampling in other estuaries was not envisaged. However, during early 1969 the St. Lucia system showed signs of becoming hypersaline and because it seemed possible that aspects of the biology of the fish might be influenced by these conditions, the programme was extended to include Richards Bay (from May 1969) and Durban Bay (from September 1969). This permitted results generally representative of the biology of estuarine fish of Natal to be obtained.

3.3 Areas of sampling

It is considered unnecessary to give detailed descriptions of the three estuarine systems where research was undertaken because this would be repetitive of the published work of Day and Morgans (1956), Millard and Harrison (1952) and Day, Millard and Broekhuysen (1954) on Durban Bay, Richards Bay and St. Lucia respectively. For purposes of acquainting the reader with these areas a brief outline of each should suffice, but mention will be made of any significant changes which have taken place subsequent to the above publications.

3.3.1 The St. Lucia Lake System (Fig. 3)

The principal features of this system have been described by Day et al (1954) and in the report of the 'Commission of Inquiry into the Alleged threat to Animal and Plant life in St. Lucia Lake' (Kriel, 1964-66). In order to facilitate studies of the dynamics of the lake system, all relevant data in the above reports as well as those data collected recently are being assembled into a comprehensive series of publications of which the first (Hutchinson and Pitman, 1973) deals with the climatology and hydrology of the system. The outline below quotes from these sources.

Physical features

The lake is a large, shallow stretch of water dotted with several islands. It is approximately 40km long and 3 - 8km wide, with a maximum width of 21km. The connection to the sea takes the form of a narrow winding channel about 21km in length and known as the Narrows. In shape the lake resembles a rough letter H of which the western limb is False Bay and the cross-bar a strait known as Hells Gates. The much longer eastern limb is constricted at Fanies Island to form St. Lucia North Lake and St. Lucia South Lake. The total lake area is about 31000ha but this varies considerably according to water level. In general the eastern shoreline is marshy and reed covered while the western shoreline is steep and wooded. The average depth below mean sea level is 0.6 - 1.2m and the maximum depth about 2m. Most of the substrate is soft mud but there are several sandy areas, particularly along the eastern shore. The entrance to the Narrows is very shallow and consists of Brodies Crossing and the excavated Potters Channel.

Four rivers drain into St. Lucia Lake, their points of entry being in those parts of the system which are most remote from the sea. The Mkuze is the largest of these and flows through an extensive swamp before entering the lake at its extreme northern end. Far to the south, the small Mpate River enters the northern Narrows. The Umfolosi River, which drains more than half of the total lake catchment, used under natural conditions to pass through an extensive swamp before entering the Narrows within a kilometre of the estuary mouth.

Hydrology

The mean annual rainfall in the immediate environs of the lake decreases from about 1125mm on its eastern shore to about 600mm west of False Bay, the mean annual rainfall over the lake surface being 890mm. Roughly 60% of this falls during the summer period October - March. Further westwards in the inland mountainous catchment the average annual rainfall increases to a maximum of 1500mm and in these areas about 80% of the rain falls during the summer period. Considerable variation in annual rainfall occurs.

Mean annual evaporation, measured by the Symons pan method, increases from about 1325mm along the lake's eastern coastal catchment to about 1490mm on the west bank of False Bay. Thus according to these estimates evaporation exceeds precipitation, the deficit being about 200mm in the east increasing to 890mm in the west.

Runoff from the catchment is required to make up this deficit. This occurs seasonally in about the proportions quoted for rainfall, but is more erratic because it is influenced by the form in which the precipitation occurs. Runoff from the eastern catchment is less variable and fulfils the very important role of supplying water in dry periods when river flow from inland catchments is reduced. Furthermore, it enters the lake in the form of seepage along the full length of its eastern shore.

In dry years runoff is inadequate to make good the net loss caused by evaporation and the lake drops to below mean sea level, thus causing sea water to flow into the system. Salt accumulates and during periods of severe drought the continued evaporation causes the salt concentration to increase to above that of sea water; the most saline conditions developing in those parts of the lake furthest from the sea. Although there is some evidence that periods of hypersalinity did occur naturally (Cholnocky 1968), man's increasing utilization of fresh water for agriculture, forestry and industry has undoubtedly reduced runoff and hence increased the incidence and severity of the hypersaline condition. Probably the single most serious event from the point of view of the hydrology of the lake, was the movement of the mouth of the Umfolosi river from its natural point of entry into the St. Lucia estuary to a new position about 1.5km to the south where it flows directly into the sea. This isolation of the Umfolosi from the lake system became necessary after its swamps had been drained and the river canalised. With the filtering action of the swamp removed, the river carried so much silt and debris into the estuary mouth that its incidence of closure increased and the Narrows became seriously reduced in cross section. The consequences for the fauna of the lake were so serious that it was decided to relocate the Umfolosi mouth. Dredging of the Narrows was also undertaken. Although this solved the siltation problem, the loss of Umfolosi water aggravated the tendency for the system to become hypersaline.

Tides do not extend into the lake but considerable water movement is induced by the prevailing north easterly and south westerly winds that blow along its length. Due to the shallowness of the water wave action prevents salinity layering and stirs up the fine sediments causing high turbidities.

Conditions during the research period (Aug. 1968 - Dec. 1971)

Salinity

Regular monthly monitoring is undertaken by the Natal Parks Board at 20 stations located throughout the system, the temperature corrected hydrometer method being employed in the salinity determinations. The data for four stations representative of different parts of the system have been graphed in Fig.4 to indicate the salinity regime during the course of the present study. The stations are as follows:

Hells Gates - representative of north lake
Fanies Island - representative of mid-lake
Charters Creek - representative of south lake
4km upstream of bridge - representative of Narrows

From Fig.4 it is apparent that there was a reversed salinity gradient in the system, with the highest levels being attained in those areas most remote from the sea. False Bay and the north lake were strongly hypersaline (40 - 97°/oo), and in comparison with the south lake exhibited greater total salinity variation (about 50°/oo), faster rates of decrease (37°/oo over the five months February to July 1969) and faster rates of increase (45°/oo during the eight months August 1969 to April 1970). Conditions in the south lake were also hypersaline for most of the period, salinities of less than 35°/oo only being recorded from March to May 1969 and in June 1971. Considerable variation in salinity occurred (23 - 59°/oo) and rapid changes were recorded. It is obvious that organisms in the northern parts of the system were exposed to more severe osmoregulatory stresses than those in the south.

In contrast to the lake, salinities in the Narrows only exceeded 35°/oo on the few occasions when outflow of of hypersaline water took place. For about half of the period salinities approximated sea water, while for 30 - 40% of the time lower salinities were recorded. These resulted when the south lake experienced lowered salinities and outflow occurred, after localised rains (particularly in the Mpate river catchment), and when Umfolosi river water was canalised into the system. The four month reduction in salinities during 1970 was caused by the temporary closure of the estuary mouth and the opening of a canal from the Umfolosi river into the southern Narrows.

Water temperature

The temperatures recorded are summarised in Table 2 and appear to be more comprehensive than any data published so far. There is little doubt, however, that the annual temperature regime could be defined more precisely if more extensive monitoring was undertaken.

Temperatures in the lake tend to be slightly higher in spring, summer and autumn, and lower in winter, than in the estuary where temperatures are influenced by the sea. The variation in mean monthly temperature is thus greater in the lake (9.3°C) than in the estuary (7.9°C), but is relatively small overall. In the lake mean monthly summer temperatures are very similar, January (27°C) being slightly warmer than December and February. June (17.7°C) appears to be the coldest month of the year.

Short term fluctuations in temperature also seem to be relatively small in the lake, the greatest range recorded being 8.5°C in January. The total annual variation recorded was 14°C for both the lake (16.5 - 30.5°C) and the estuary (16.0 - 30.0°C). However, in the marginal shallows greater total variation occurs, temperatures of 15.0 - 34.5°C having been recorded.

These data confirm previous records from St. Lucia (Day, Millard and Broekhuysen, 1954; Millard and Broekhuysen, 1970) and show that the temperatures at St. Lucia are very similar to those recorded for Richards Bay (Millard and Harrison, 1952; Hemens, 1970; Hemens et al, 1971) and the Umlalazi lagoon (Hill, 1966). Winter temperatures in the Umlalazi (July 15.0 - 18.5°C) are however slightly lower than have been recorded in St. Lucia. From a review of the published temperature data on Natal estuaries it has become obvious that data are inadequate to permit adequate comparison between estuaries and determination of whether there is any significant increase in temperature with reduction in latitude.

Water turbidity

The waters of the lake are generally turbid as can be seen below :

Seasonal turbidities (mm) recorded at the standard netting sites in the south lake by means of a 20 cm secchi disc (used according to Welch, 1948).

SEASON	MEAN	N	RANGE
Summer (D,J,F)	359	9	185 - 670
Autumn (M,A,M)	515	17	265 - 965
Winter (J, Jl, A)	562	18	210 -1000
Spring (S, O, N)	477	9	115 - 730

The most turbid conditions occur during spring and summer and are associated with the strong north easterly and south westerly winds which stir up the fine sediments by wave action. Thus the upper levels in the ranges recorded are usually found in the areas of coarser substrates on the eastern side of the lake.

Aquatic vegetation

When there is a normal salinity gradient a rich aquatic flora exists in the lake. Submerged macrophytes consist of eel grass (*Zostera capensis*) in the south lake at salinities of 30 - 35‰, and *Ruppia spiralis* and *Potamogeton pectonatis* at progressively lower salinities towards the north. Marginal vegetation extends into the shallow water and consists mainly of reeds (*Phragmites communis*) and sedges (*Scirpis* sp.). This prolific flora produces large quantities of detritus and thus plays a very important role in the ecology of the system.

Under the hypersaline conditions prevalent during the study period the aquatic vegetation became greatly impoverished. None of the submerged macrophytes survived and the marginal vegetation consisted of reeds which did not extend into the lake other than in a few areas on the eastern shore where there was freshwater seepage. Clearly salinities had exceeded the levels of tolerance of the aquatic vegetation.

In the Narrows extensive dredging and deposition of spoil on the banks has destroyed at least half of the natural gently sloping tidal mudbanks and hence reduced the area suitable for the growth of mangroves. Formerly three species (*Rhizophora mucronata*, *Avicennia officinalis* and *Bruquieria gymnorhiza*) formed a dense forest along the south bank of the estuary in the vicinity of the Umfolozi mouth, but this has subsequently been killed by dredging. Small patches of mangroves do still occur in the Narrows and *Rhizophora* is common in the western fork south of Brodies Crossing. Reeds extend to the waters edge.

Aquatic fauna

The aquatic fauna is very rich and because the area is administered as a wildlife sanctuary, includes a spectrum of species which is more diverse than any other found in South Africa and which is no longer represented in more than a few estuarine systems in Africa. Papers by Day *et al* (1954) and Millard and Broekhuysen (1970) describe and list the fauna, so only a brief outline will be given here.

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A total of 113 species of invertebrates has been recorded. Special mention should perhaps be made of the large number of swimming prawns (Penaeidae) which migrate between the lake and the sea annually, as well as the variety of crabs (26 spp.) which includes the large swimming crab Scylla serrata. Aquatic birds are particularly abundant when conditions are favourable and the total of about 60 species includes duck, waders, gulls, flamingoes, terns, herons, cormorants, pelicans, osprey and fish eagles. Many of these prey on fishes, especially juveniles. The Nile crocodile occurs throughout the system. Approximately 600 hippopotami still play their natural role in the ecology of this estuarine system. Elasmobranch fishes occur in the Narrows and the south lake and include a skate (Dasyatis uarnak), the 'maneating' zambezi river shark (Carcharhinus leucas) and sawfish (Pristis pectonatus), which has been recorded up to 5m in length. (When pulling a net waist-deep in the lake some of these last mentioned organisms tend to be considered 'predatory' by the fisheries biologist).

A total of 103 species of teleost fish has been recorded (included in Table 1). This consists mainly of euryhaline forms because the tidal influence does not extend into the lake and stenohaline marine species are unable to penetrate far into the system. Most species are migratory and only spend certain periods of their lives in the lake. There is therefore much movement in and out of the Narrows. Under normal circumstances the lake supports an exceedingly rich fauna and there can be no doubt that on the East Coast of South Africa it plays a very important role in the maintenance of stocks of those species which benefit from an estuarine phase in their life cycles. Despite the hypersaline conditions during the study period, fish were remarkably abundant and even under these circumstances St. Lucia is considered to have supported a greater estuarine fish population than any other estuarine system in Natal. The ability of many species to adapt to the extremes in salinity that prevailed constitutes an interesting aspect of their biology.

3.3.2 Richards Bay (Fig.5)

This sub-tropical estuary is situated south of St. Lucia on the Zululand coast (28°48'S, 32°05'E). During the period of research it was in its natural state, had an area of 2987 ha and was administered by the Natal Parks Board as a wildlife sanctuary. Its topography, physico-chemical characteristics and ecology have been described by Millard and Harrison (1952), Hemens (1970) and Hemens *et al* (1971).

Prior to January 1972 the system consisted of the main bay with a maximum width of 6.3km and a much narrower winding channel linking it with the sea. It was fed by numerous rivers (of which the Umhlatuze and Umzingazi were the largest) which ensured that the mouth was permanently open and that a normal salinity gradient existed. Salinities in the bay generally ranged from 15 - 30‰ depending on fresh water inflow conditions, but greater variation occurred after droughts when levels rose to approximately 35‰ and after floods when they dropped rapidly and became virtually fresh for short periods. The bay was shallow (0.9 - 1.25m) and experienced little tidal rise and fall due to its size relative to that of the channel and mouth. The bottom was mainly fine mud but became a sandy mud in the channel and sandy near the mouth. The water was usually turbid in the bay where secchi values of 25 - 620mm were recorded and 100 - 500mm were common. Water temperatures were similar to St. Lucia.

Submerged macrophytic vegetation consisted mainly of eel grass (*Zostera capensis*) which was abundant in the channel (Fig.5). Marginal vegetation was largely made up of mangrove forests (*Avicennia officinalis*, *Rhizophora* *mucronata* and *Bruguiera gymnorhiza*) along most of the eastern shore of the system and in patches elsewhere; as well as reeds (*Phragmites communis*) which did not stand in the water as it was too saline.

Shortly after the research programme was completed a start was made in the conversion of Richards Bay into a modern harbour catering for bulk carriers of up to 150 000 tons. Extensive changes are therefore taking place, of which the major ones consist of the division of the bay by a SE/NW berm wall into a southern sanctuary with a new artificial mouth, and a northern harbour served by a greatly enlarged access channel to the sea. The aim is to establish estuarine conditions in the sanctuary similar to those previously found in Richards Bay as a whole and to isolate the sanctuary from the pollution of the harbour. It is encouraging that enlightened planning is making it possible to protect about half of the total area of Richards Bay from the environmental devastation so common in harbours and so evident in neighbouring Durban Bay.

3.3.3 Durban Bay (Fig.6)

Durban Bay (29°52'S, 31°02'E) has an area of 1061 ha, length of about 5.5km, width of 3km and is connected to the sea by the narrow harbour entrance. It is today primarily developed as a harbour and is surrounded by the city of Durban. There has been a serious decline in its former biological wealth due to consolidation of banks into wharfs, dredging of sandbanks into turning basins and as a result of pollution from the city. Nevertheless a surprisingly rich fish fauna persisted during the study period.

A detailed account of the system as it was in the early 1950's is provided by Day and Morgans (1956) who point out that it is a bay and not an estuary as the salinity is essentially that of the sea. However, in his paper on the origin and distribution of estuarine animals in South Africa, Day (1966, p.164) makes the point that: 'Estuaries are not only areas where the salinity is reduced, they also differ from the open shore in regard to the strength of wave action and type of substratum'.

In these respects Durban Bay certainly contrasts markedly with the shallow inshore zone of Natal which is battered by persistently heavy surf and where the intertidal beaches consist of coarse shifting sand. As a result it contains many species which are common in neighbouring estuaries but are not found in the open sea, the best example probably being the extensive mangrove community which used to flourish along its southern shores.

The similarities in the physical environments of Durban Bay and Natal estuaries are reflected by close affinities in their fish faunas. Thus although the stenohaline marine component is better represented in Durban Bay than in true estuaries, its fauna consists to a large extent of typically euryhaline fishes and of those stages in their life cycles (particularly juveniles) which normally abound in the estuarine environment. Thus the data collected in Durban Bay have been presented together with those obtained from Natal estuaries, but care has always been taken to scrutinise the data for deviations which might arise due to the physical conditions specific to this environment.

3.3.4 Miscellaneous Natal estuaries

Sampling was also conducted irregularly in the Kosi lakes and in the estuaries of the Umlalazi, Sinkwazi, Amatikulu and Umhlanga rivers.

3.4 Sampling procedures and net specifications

3.4.1 Biology of adult fish in the estuarine environment

Most sampling was done by means of gill netting because this technique had certain distinct advantages. Gill nets fish continuously from the time they are laid until they are lifted, the extent of the catch being related to the amount of fish movement in their vicinity. Consequently it is possible to sample throughout a 24 hour period and to avoid bias caused by diurnal behaviour or activity patterns. Thus gill net catches provide not only qualitative information on what species occur in an area, but if the catch is expressed in terms of some unit of fishing time, quantitative data as well. The latter is difficult to achieve by other netting techniques (such as seine netting) and is extremely valuable as it makes it possible to investigate localised or seasonal fish abundance. Other advantages of gill nets are that they can be set in the middle of large stretches of open water, in a range of water depths, and in addition, can be operated by only two or three men in a single boat.

The main disadvantage of gill nets is that any particular mesh tends to capture fish within a restricted size range, there being both lower and upper limits of size beyond which the probability of capture is low. Thus a fish is only susceptible to capture between the size at which its maximum girth slightly exceeds the internal perimeter of the mesh, and the size at which it becomes too big to penetrate the mesh far enough to become caught. In order to sample the estuarine fish fauna over its adult size range it was found necessary to use five different mesh sizes with overlapping ranges of selectivity.

Gill nets were designed to withstand two years use in an environment where they were prone to capture large crocodiles, sharks and sawfishes; would probably entangle hippopotami; as well as catch fish of a wide range of species. For this reason and because it was originally hoped to undertake a tagging programme that required minimum damage to captured specimens, relatively thick twine was used. An advantage was that net damage and repairs were kept within reasonable limits. However, since gill net efficiency decreases with increasing twine thickness, catch rates were reduced and considerable netting effort had to be expended on occasions to obtain an adequate sample. It must therefore be pointed out that although the catch rates provide a measure of relative abundance from month to month, they underestimate the number of fish that can be caught per unit time and should not be compared with catch rates recorded in gill netting studies elsewhere.

All gill nets were of similar size and construction, varying only in mesh size and twine thickness. Two nets of each mesh were made up. Details as follows:

length 45.7m (150ft.); depth 1.8m (6ft.); headrope, footrope and gables of 40mm circumference polyethylene; floats of vinyl chloride, bouyancy 1700gm, spaced 2m apart; stapling regular with 2 meshes per staple; lead sinkers of 275 - 550g, spaced 1m apart; other details:

Stretched mesh size (cm)	Braided nylon twine	Duration of use
5	210/18	Feb.1969-Dec.1970
7	210/24	Sept.1969-Dec.1970
9	210/27	Feb.1969-Dec.1970
13	210/60	Aug.1968-Dec.1970
18	210/72	Feb.1969-Dec.1970

Routine monthly sampling trips were undertaken to St. Lucia estuary, St. Lucia south lake and Richards Bay; two or three nights being spent at each locality.

At St. Lucia estuary nets were set in the Narrows between the bridge and the Mpate river. Due to the riverine character of this area they were set across the channel, either singly or in pairs, the smaller mesh nets being placed in shallow water where better catches of small fish were made. This arrangement meant that the nets intercepted fish moving up or down the Narrows and provided a quantitative estimate of their abundance from month to month. As this is the only migration route between the lake and the sea, data on the seasonal migrations between these environments were obtained.

In the open waters of St. Lucia south lake the nets were usually set in two extended 'trains', each with a total length of 228·5m (750ft.) and consisting of the full sequence of mesh sizes. A standardised netting routine was adopted whereby the best fishing areas were always sampled first; these being off Charters Creek, off the eastern shores from a point opposite Charters Creek and stretching south eastwards as far as the Nkambazana river, and off the north eastern shore of Mitchell Island. On occasions when these localities yielded poor catches netting was extended over a wider area in order to obtain an adequate sample.

Due to the need to limit fieldwork to 7 - 10 days per month it was unfortunately impossible to undertake regular netting in the north lake. However, in order to obtain a general understanding of the fish fauna of the St. Lucia system, sampling of the populations in the north was essential and was carried out on frequent occasions. This resulted in netting being undertaken in most parts of the north lake over the 1969/1970 period and provided data on the length composition of the fauna, its upper tolerances of salinity and other parameters which supplemented the basic study conducted in the south.

In Richards Bay gill netting was conducted in a standard area situated in the vicinity of the channel that stretches westwards from Treasure Island towards the mouth of the Umhlatuze River. Netting was frequently conducted elsewhere in the system. In addition, catches taken in the Natal Parks Board mullet seine were examined during the course of most monthly visits. This provided general coverage of the bay as seining is carried out wherever mullet are plentiful.

In Durban Bay gill netting was not possible due to shipping movements and sampling had to be restricted to seine netting. The net was always shot from a boat in the Salisbury channel and pulled out onto the adjacent sand banks. Details of the net are as follows:

total length 172m; depth in bag 5m and in wings 3-5m; width of mouth of bag 14m, tapering to 3.3m; mesh 10cm stretch tapering to 5 cm in wings, and 3cm in bag.

Plankton netting for fish larvae was conducted in the St. Lucia system as this formed another method of assessing whether spawning occurs under estuarine conditions (details are given under 3.4.2).

Data collected in association with each netting operation consisted of: date, locality, type of gear, duration of netting, the number of specimens of each species caught, water temperature range from maximum/minimum therometer submerged with the net, water depth, salinity, turbidity and wind strength and direction.

3.4.2 Biology of juvenile fish in the estuarine environment

During 1969 and 1970 some juvenile sampling with drag nets was undertaken in conjunction with the adult programme, the object being to obtain the experience necessary for planning the intensive research scheduled for 1971 and to extend the juvenile study over a period of three years. Plankton netting was carried out in order to sample larval and post-larval fishes.

From this preliminary work it became apparent that a wide variety of different types of netting gear would be required if the juvenile phase was to be adequately sampled over the size range from first recruitment to the limits of selectivity of the gill nets used in the adult programme. It was also clear that the gear would have to be effective in a variety of habitats, inclusive of the marginal shallows and deeper open water areas. Although quantitative sampling would have been desirable, most techniques could not be adequately standardised to provide reliable results. For example, it was not possible when sampling in various localities with drag or seine nets to standardise conditions such as distance covered or duration of operation. This is due to variation in such factors as the softness of the bottom substrate, water depth, the extent of aquatic vegetation and the spacing of points of access to and egress from the water. Furthermore, the 'hit and miss' characteristic of this type of sampling often makes it a matter of luck whether or not a shoal is surrounded by the net. Experience in the field did, however, provide a general indication of the relative abundance of the different species.

The intensive programme lasted from January 1971 to March 1972, regular monthly sampling being carried out in St. Lucia estuary, St. Lucia south lake and Richards Bay. Supplementary netting on an irregular basis took place in Durban Bay, the Zinkwazi, Amatikulu and Umlalazi rivers, and in the Kosi Lake system. During November 1973 the coverage of East Coast estuaries was greatly expanded by a survey that extended southwards to Cape Agulhas and around to the Atlantic West Coast estuary of the Berg river. The object of this survey was to plot the geographical extent of utilization of estuaries by the juveniles of species common in Natal. The estuaries included in the juvenile programme are shown in Fig.2.

At St. Lucia and Richards Bay netting was conducted at selected localities where the fish were usually abundant or where their occurrence was of particular interest. These were as follows:

St. Lucia (Fig.3)

(i) between the mouth and Honeymoon Bend
(ii) in Potters Channel
(iii) at Charters Creek
(iv) along the eastern shore of the south lake between Nkambazana River and Catalina Bay.

Netting was also conducted in most other parts of the lake, particularly along its eastern shore as far north as Sengwane.

Richards Bay (Fig.5)

(i) in the eel grass (Zostera capensis) beds located near Spinach Point.
(ii) adjacent to the mangrove communities lining the eastern shore of the bay.

The sampling procedure was standardised as far as possible by ensuring that each type of gear was used each month, but no attempt was made to standardise netting effort. This was because the object of each collecting trip was to obtain a representative sample and effort was consequently highest when the shoals were difficult to locate, when the fish were not abundant or when weather conditions made their capture difficult.

Details of the netting gear and methods of sampling the different growth stages are outline below:

Larvae

Surface plankton netting was carried out on one night per month at St. Lucia estuary (within 4km of the mouth) and in the southern lake off Charters Creek from January 1969 to December 1970. Meshes 32 per cm; mouth diameter 45cm; length 1m.

Larvae, post-larvae and small juveniles

A so-called 'box-net' was towed at higher speed in the bow wave of the boat as it was thought that

faster moving forms might be able to avoid the plankton net.
Mesh 0.32cm stretch; consisted of a box frame of reinforcing rod with a mouth of 30 x 45cm and sides of 64cm, tapering towards the rectangular back of 18 x 32cm.

Scoop nets were used during the day and at night, both from a boat in open water and while wading in the marginal shallows.
Mesh 0.32cm stretch; consisted of a bag mounted on a circular frame of 50cm diameter, attached to handles 1 - 3m in length.

Juveniles

Commercial trawling for penaeid prawns is carried out by the Natal Parks Board at St. Lucia in the vicinity of Potters Channel. As this is the main route of access from the sea to the lake, the catches of juvenile fish provide information on recruitment into the system. These catches were monitored during the years 1969 to 1971. Experimental sampling with similar gear was conducted in other parts of the southern lake in depths of 0.5 - 1.7m. Mesh 2.5cm stretch. The gate net trawl consists of a rectangular frame 3.7 x 1m which supports a net 5m in length. Two skids on the lower bar allow it to be dragged across the bottom by an outboard-powered dinghy.

Drag netting was conducted in the marginal shallows at night and during the day.
Mesh 1.27cm stretch; length 6.1m; depth 1.83m; 1.83m tapered purse; dragged by two men.

Seine netting was restricted to the marginal shallows and around islands.
Mesh 1.27cm stretch; length 30.5m; depth 2.74m; purse tapers from 9.14m to 3.05m over a length

of 9.14m; pulled by two or four men.

'Cast' netting was usually limited to areas where crocodiles were so abundant that it was extremely dangerous to enter the water. These nets were also used for capture of small fish on the surface of open water. Two nets were used with mesh of 1.27cm and 3.18cm stretch; diameter 3m and length 2m.

In addition to the above, small mesh gill nets (mesh 38mm, 51mm, 65mm stretch), juvenile fish traps and larval fish traps were used initially. These gear proved to be impractical and were abandoned after a trial period.

3.4.3 Biology in the marine environment

Sampling of this phase of the life cycles was conducted during 1972/1973 and involved monitoring the catch of shore and ski-boat anglers, as well as of commercial trawlers when this was possible.

Extensive beach patrolling using a 'beach buggy' was conducted over weekends and during early morning and evening hours so as to coincide with periods of most intense sport fishing effort. Attendance of fishing competitions also provided many valuable specimens. In order to stimulate the cooperation of anglers the research was publicised in the press and on the radio. Monthly circulars reporting interesting research findings were sent to all Natal angling clubs. In this way considerable interest was engendered amongst anglers and they soon became keen to assist by making their catches available for dissection. Samples obtained in this way were supplemented by purchasing specimens brought to the Institute.

This programme resulted in useful data being collected from the inter- and immediate subtidal zone along the Natal coast. Although much of the catch was hooked within casting distance of the beach, in the Durban area fish were obtained from slightly further out as a consequence of fishing from various groynes, a jetty near the Institute and the piers that extend out to sea to protect the harbour entrance. Catches taken in a commercial seine net operated on the Durban beachfront and in beach nets from Inhaca Island (off Lourenco Marques), were also examined.

Sampling of deeper areas was less intense and consisted of the examination of the catches of ski-boats which are launched through the surf from Natal's sandy beaches and operate from just beyond the surf zone down to depths of about 70m. Catches were sampled irregularly from a number of points between Durban and Sordwana Bay.

Shallow water commercial trawling is limited in Natal and unfortunately no research vessel was available for this purpose. Sampling was thus opportunistic and involved the examination of commercial catches on the relatively few occasions when this was possible. Samples were obtained from the Tugela banks in 30-40m and from a small ground off St. Lucia mouth in 40m. Catches taken by shrimp trawlers operating in depths of 4 - 10m in Delagoa Bay were also examined. In all cases some species were encountered which had also been recorded in estuaries. Not unexpectedly, catches taken by lobster trawlers in depths of 320 - 460m on the Natal coast did not include any species known to occur in estuaries.

4. THE ESTUARINE FISH FAUNA

4.1 Species composition of the fauna of Natal and the species included in the research programme

The marine fish fauna of the East Coast of South Africa is extremely diverse, and since the estuarine fauna consists basically of marine species able to tolerate variable salinity conditions, it is understandable that the fauna of East Coast estuaries also exhibits considerable diversity. This is apparent from Table 1 which lists alphabetically the species recorded during the course of ecological surveys and the present programme. Some of the species in the checklist have not been recorded in the present study and in these cases the identifications published by previous workers have been accepted.

An impressive total of 232 species has been recorded and comprises stenohaline, euryhaline and freshwater components. For ease of discussion the number of species in each component is summarised below.

Number of species in each of the major components represented in the fish fauna of Natal estuaries

	Stenohaline	Euryhaline				Fresh-water
		Rare	Common	Very Common	Abundant	
Number of species	116	61	35	7	10	3
Total	116	113				3

It is apparent that half of the total number of species consists of stenohaline forms which only occur in those parts of estuarine systems close to the sea where there is no reduction in the salinity of the environment. These are in fact inshore marine species which are unable to cope with the osmoregulatory stresses of lowered salinities and are thus ecologically distinct from estuarine forms. For this reason the stenohaline component is not considered part of the estuarine fauna and will not be considered further in this thesis.

At the other extreme is the freshwater component consisting of three species, which unlike most of their contemporaries are able to penetrate the saline waters of estuaries. Their recorded salinity tolerances vary considerably, the most remarkable species being Tilapia mossambica which has been sampled in St. Lucia Lake at salinities in excess of 110‰! In view of their ability to penetrate saline estuarine waters inclusion of these species in the estuarine fauna seems justified.

The euryhaline component, comprising a total of 113 species, has been divided into four sub-groups representing different frequencies of abundance. Slightly more than half this number (61 species) has been found to be rare in Natal estuaries. About 20 of these are typically marine species, which being predatory by nature and able to tolerate reduced salinities, occasionally enter estuarine waters to feed on the small fishes which abound. Examples are the sea pike Sphyraena spp., kingfish Caranx spp., rock cods Epinephelus spp. and the elf Pomatomus saltatrix. Approximately another 20 species are also typically found in the marine inshore environment and only rarely occur in Natal estuaries. Examples are the blacktail Diplodus sargus, karanteen Crenidens crenidens, concertinafish Drepane punctata and the striped mullet Liza tricuspidens. Other species owe their rarity to the fact that the Natal coast is near the limit of their geographic range so that they only occur here infrequently or in reduced numbers (see Section 4.2).

The additional three sub-groups recognised within the euryhaline component (and comprising the remaining

52 species in the checklist) have been rated as common, very common and abundant. It is these species, and particularly those in the last two sub-groups, which out of the total of 232 species actually constitute the dominant part of the estuarine fish fauna. Our studies were concentrated on these sub-groups, but in view of the greater need for management of species of direct significance to man, special attention was paid to sport angling species such as the spotted grunter (Pomadasys commersonni, Natal stumpnose (Rhabdosargus sarba), and kob (Argyrosomus hololepidotus); as well as to non-angling species with food production potential such as the mullets Mugil cephalus, Liza macrolepis and L. dumerili (these and other species that received detailed attention are illustrated in Fig.7).

4.2 Distribution

As a background to these studies it is interesting to examine the distribution of the dominant part of the fish fauna (as outlined above) and of those species which are rare in Natal due to being near the limits of their distributional range. Problems arise in trying to do this as some species are difficult to sample in the field and records for them are consequently less comprehensive. These have been excluded from Fig.8 so as to avoid confusing the general patterns of distribution which can be deduced from the better known species.

In the figure the sampling localities and regions of the coast have been spaced in proportion to the true distances that separate them. The exception is the section representing the tropical Indo-Pacific region which has been foreshortened for obvious reasons. It should be pointed out that the continuous lines representing each species incorporate the extreme ranges of distribution that have been recorded; the normal range usually falling well within these limits. Sources of information have included the publications and original raw data of the Dept. of Zoology, University of Cape Town, and the J.L.B. Smith Institute of Ichthyology, Grahamstown; which were kindly made available by Professor John Day and Mrs. Margaret Smith respectively. These data were supplemented by the research results obtained by the Oceanographic Research Institute. The localities of sampling are indicated on the map of southern Africa (Fig.2).

A fact which is immediately apparent is that most species are tropical and sub-tropical Indo-Pacific forms and that the East Coast of South Africa represents a subtraction margin in their distribution. Some species have their southerly limit of distribution in Natal (e.g. the pursemouth *Gerres oblongus*, the mullet *Valamugil cunnesius*, and the grunter *Pomadasys multimaculatum* and the needlefish *Tylosurus crocodilus*). A large number of species reach their limits of distribution along the stretch of coast between the Transkei and the Swartkops river (near Port Elizabeth); while only relatively few extend further west along the South Coast of the country. It is clear that certain environmental factors will therefore have a bearing on their biology in this region. The most obvious factor is the reduction in water temperature towards the south west. The importance of its role can be deduced from the fact that many species only occur towards the south western limits of their range during the warm summer months. Examples are the spotted grunter (*Pomadasys commersonni*), Natal stumpnose (*Rhabdosargus sarba*) and the springer (*Elops machnata*) (Smith 1950; Smith 1961). This pattern of distribution can be readily understood from the similarity between winter temperatures in the north east and summer temperatures in the south west, which is apparent from the figures over (after Bass *et al* 1973, Table 1):

Locality (see Fig.2)	Mean water temperatures (°C) Winter	Summer
Oro Point (on N.E. border of South Africa)	21	26
Durban	19	24
Port Elizabeth	16	22
False Bay (South of Cape Town)	13	18

An additional limitation to any lengthy sojourn by sub-tropical species on the South Coast is the sudden onset of very cold conditions which takes place occasionally during summer or autumn as a result of upwelling. This can reduce temperatures from the region of 20°C to as little as 10°C in the matter of a day (Smith, 1949; Day 1951; Korringa, 1956) and causes mortalities amongst less hardy species (more details in Section 6.4).

With the exception of events such as that described above, temperatures in estuaries tend to fluctuate more than at sea and this is particularly true towards the head of the estuary where there is river inflow. The season of rainfall and hence river flow is thus important. In South Africa this changes progressively from being in summer in the north east, to winter in the south west. As many South Coast rivers drain mountainous catchments having predominantly winter rainfall, estuarine temperatures tend to be low. Temperature induced variations in seasonal abundance are therefore likely to occur when species are near the limits of their adaptive range.

Another major feature apparent from Fig.8 is that a number of species are South Coast forms which extend up the West and East Coasts for varying distances. These tend to be endemics which have evolved in the rather specialised environmental conditions characteristic of this region. Examples of species which infrequently extend as far as Natal are the white stumpnose (*Rhabdosargus globiceps*) and the white steenbrass

(Lithognathus lithognathus), while those that occur in Natal waters include the Cape silverside (Hepsetia breviceps), halfbeak (Hyporhampus knysnaensis), the Cape stumpnose (Rhabdosargus holubi) and the mullet (Liza tricuspidens, Myxus capensis and Liza alata).

In addition there are a few species which are temperate-eastern-Atlantic in distribution and which extend as far as the Transkei (e.g. Liza richardsoni) and into the warm waters of the East Coast, for example the kob (Argyrosomus hololepidotus) and leerfish (Hypacanthus amia).

As would be expected, the temperate species in these latter groups extend further and are more abundant on the East Coast during the cooler months of the year.

Finally, a particularly important species of fish which is abundant in South African estuaries and merits special attention is the grey mullet, Mugil cephalus. This cosmopolitan species occurs between 42°S and 42°N (Thomson, 1963) and owes this remarkable distribution to its hardiness and tolerance of wide ranges of environmental conditions.

From the foregoing it can be seen that the estuarine fish fauna comprises four main faunistic components, namely:

(i) tropical and sub-tropical Indo-West-Pacific species which make up the bulk of the fauna, particularly in Natal.

(ii) temperate endemic South Coast species which extend into East Coast waters.

(iii) temperate-eastern-Atlantic species.

(iv) cosmopolitan species.

The estuarine fish fauna thus includes the four main components distinguished by Stephenson (1947) in the South African shore fauna and flora, as well as the components recognised in shallow water by Smith (1949) in his study of the sea fishes of southern Africa.

4.3 Response to conditions of hypersalinity

It has already been explained that St. Lucia lake became increasingly hypersaline during the study period and that the highest salinities occurred in the northern parts of the system (Section 3.3.1 and Fig.4). During the course of sampling interesting information was obtained on salinity tolerance levels and on the response of the fish fauna to these conditions.

A summary of the salinity ranges of species commonly caught in gill nets is provided in Fig.9. This shows that some species can adapt to extremely high salinities: T. mossambica (a 'freshwater' fish) and E. machnata were recorded at more than 110‰, and M. cephalus and R. sarba at above 80‰. It is significant that 10 species had their upper limits of distribution within the salinity range 65 - 75‰. Although this is likely to result from osmoregulatory problems experienced by the fish themselves, a survey of the benthos in the north lake (Wallace, 1969) revealed that very important molluscan food organisms such as Solea corneus, Eumarcia kochii and Nassarius kraussianus were killed by salinities of 65 - 70‰. There is therefore evidence that the distribution of the fish fauna is also likely to be influenced by the availability of food. The remaining species in Fig.9 were recorded at decreasing salinity levels, with L. equulus (and others not figured) apparently not occuring at above 35‰.

From the above it can be deduced that as salinities rise in the north lake the number of species that occur in the area will become reduced. In fact this trend can be demonstrated by relating salinities in the north lake to the number of species of fish recorded there during the course of surveys by the University of Cape Town and the Oceanographic Research Institute (Fig.10). These data show that high salinities are associated with a reduction in the species diversity.

Some interesting observations were made in the very hypersaline areas of the lake. For example, the relatively few specimens of P. commersonni and R. sarba recorded at levels in excess of 70‰ were no longer able to feed on their normal molluscan and crustacean food and were feeding 'opportunistically' on filamentous algae (Enteromorpha) and cyanophytic algae (Oscillataria and Spiralia). Effects of reduced competition within the fish fauna were also observed. The 'freshwater' species T. mossambica, which is normally rare in estuaries due to competition from estuarine fishes, became extremely abundant throughout the north lake. It appeared to breed successfully under hypersaline conditions because large numbers of juveniles were sampled in areas remote from rivers and sources of fresh water (the rivers were not flowing due to the drought and were hypersaline in their lower reached due to 'backflow' from the lake). Other species that were abundant at salinities in excess of 70‰ were benthic feeders like the mullet M. cephalus and the milkfish Chanos chanos.

Fish mortalities, as evidenced by sightings of dead specimens, were rare despite the extremely hypersaline conditions that prevailed during 1969/70 and it is apparent that the fish population generally moved southwards to alleviate stress before conditions in the north lake became lethal. When mortalities did occur they generally followed sudden periods of cold weather and involved relatively small numbers of specimens. Species affected were A. hololepidotus, M. cephalus, P. commersonni, P. hasta and R. sarba. A probable explanation is provided by the experimental work of Blaber (1973) on the temperature and salinity tolerances of Rhabdosargus holubi (reproduced in Fig.11). It is apparent that with increase in salinity this species' range of temperature tolerance becomes reduced. Thus whereas a drop from 18 to 12°C would not have caused a mortality at a salinity of 30‰, it would have resulted in 100% mortality at 60‰. The physiological explanation for this seems to be that enzymatic rates are reduced at lower temperatures, with the result that there is a reduction in ionic efflux and an increase in the osmotic concentration of the body fluids (Prosser _et al_, 1970; Maetz and Evans, 1972). Thus when a fish is already close to its upper limit of salinity tolerance a temperature-induced reduction in osmoregulatory efficiency can result in an elevation of ionic concentration to above the lethal level for the species.

The movement of fish away from the north lake in response to the hypersaline conditions would be expected to increase fish abundance in the south but marked increases in gill net catches were not recorded. The explanation is probably that increases did occur but were not sufficiently dramatic to be detected by this method of sampling. Only in the case of _A. hololepidotus_ (Fig.12) was it possible to discern an increase in catch (in the 13cm net) in the south during periods of very high salinity in the north, and a tendency for the fish to redistribute towards the north (causing catch rates to drop in south) when salinities became less extreme. This trend was not reflected in catches in these nets in St. Lucia estuary, where changes in abundance recurred annually and seemed to be related to some cyclical event in the biology of the species rather than to salinities in the north (Fig.16, Section 6.3). This also applies to changes in abundance of the other species for which data are available (Figs.15 and 16).

From the above it appears that the very saline conditions in the north lake did not have marked consequences on the biology of the main species in the southern parts of the system. This is probably attributable to the fact that salinities in the south lake remained well within their range of tolerance and that salinities in the Narrows and estuary generally ranged between 25 - 35‰ (Fig.4), which is typical of the lower reaches of most estuarine systems. The results obtained from sampling in these areas, together with the data from Richards Bay and Durban Bay, are therefore considered to provide a good indication of the estuarine phase of the biology of these species.

5. LENGTH COMPOSITION, RELATIVE ABUNDANCE, AND DISTRIBUTION IN THE ESTUARINE AND MARINE ENVIRONMENTS

5.1 Introduction

Knowledge of the length composition of the estuarine phase of the life cycles of the various species is basic to any consideration of their biology in this environment. It not only provides insight into whether both juvenile and adult stages are represented, but if sampling is adequate, can indicate what length ranges are most abundant. Furthermore, it forms the background against which to assess the interrelationship between the estuarine and marine phases of the life cycles.

5.2 Methods

Total length was taken with the fish lying on its side on a measuring board and with the upper caudal rotated down to the mid-line. Conversion to standard and fork length can be effected for M. cephalus, P. commersonni and R. sarba by means of the regression equations in Table 3a.

Due to the variations in size of the different species, length composition has been analysed in terms of 10cm, 5cm, 4cm or 2cm length classes. This keeps the number of classes in each species within the range (15 - 25) recommended by Laevastu (1965). In each length class the number of specimens has been expressed as a percentage of the total sample, but in samples of less than 50 specimens the actual number has been plotted.

In the main species being investigated the data have been analysed separately for the St. Lucia lake system, for other Natal estuaries and for the marine catch (Fig.13). In the other species all estuarine data have been lumped and are presented in Table 3b, which includes their marine length composition, estimates of relative abundance and comments on estuarine and marine distribution. This methods has been adopted as it is a succinct means of providing an interpretation to the data obtained.

In Section 3.4 the routine netting programme was outlined and it was explained that a considerable amount of additional netting was conducted outside the standard areas in order to reduce the possibility of bias through patchiness of sampling. Furthermore a variety of different netting gear was used in an attempt to sample the fish population over its complete length range. Despite these precautions however, differences in gear selectivity can cause the composition of the sample to differ from the true composition of the population. Thus good catches of certain length classes represent positive proof of their occurrence in an area but their relative importance can be exaggerated if they are more susceptible to capture than others. To some extent this source of bias can be assessed by reference to the gear selectivities set out in Fig.14. On the other hand poor catches of particular length ranges are more difficult to analyse. These can arise from a genuine scarcity in the population, from deficiencies in sampling or from a combination of both. In the absence of detailed information concerning aspects of the dynamics of the population such as mortality in the estuarine environment or emigration from it, a detailed assessment of the reasons for the poor catch cannot be made. The approach adopted has been to consider whether sampling effort was adequate for the length range in question, and if this was deemed to be the case, to attribute the scarcity in the sample to some reduction in abundance in the population. Although there is an unavoidable element of subjectivity inherent in this, it is considered justified provided it is restricted to contributing towards a general interpretation of species length composition.

5.3 Results

Mugil cephalus

(i) St. Lucia lake system

Catches include specimens from the smallest length class (0 - 4cm) up to 68 - 72cm (Fig.13). Large specimens of about 40 - 64cm predominate in the sample as they are seasonally very abundant in the south lake and Narrows where they were caught in large numbers in the course of the standard monthly gill netting programme. However netting in the north lake revealed that juveniles were abundant in this area and the species is therefore considered to be well represented throughout the length range recorded.

(ii) Other Natal estuaries

The catch included a similar length range to that of St. Lucia but specimens less than 8cm and of 28 - 40cm made up a greater proportion of the sample. The latter is at least partly attributable to the selectivity range (Fig.14) and efficiency of the seine nets which were used in Richards and Durban Bays but not at St. Lucia. Large adults (44 - 68cm) constituted a much smaller proportion of the catch at these localities despite being subject to capture in the gill nets (9cm and 13cm) and seine nets. They can thus be considered less abundant in these systems.

(iii) Marine environment

A poor sample was obtained due to difficulties in netting under heavy surf conditions. However sightings indicated that the largest length classes are well represented off St. Lucia and along the Zululand coast. Sexually mature specimens are also netted in a beach seine operated along the sheltered Durban beaches.

Pomadasys commersonni

(i) St. Lucia lake system

The catch included a continuous length range from the 0 - 4cm length class to that of 76 - 80cm. Juveniles of 4 - 16cm predominated, while adults of 40 - 56cm which enter the system during the annual grunter 'run' (see Section 6.3) were also abundant in the sample. Routine and exploratory netting failed to reveal the presence of large numbers of intermediate specimens of 16 - 40cm and it appears that this length range is less common in the lake.

(ii) Other Natal estuaries

The catch covered a smaller overall length range, the largest specimens falling in the 56 - 60cm length class. As in the case of St. Lucia, juveniles formed the dominant component of the catch but in contrast to St. Lucia large adult specimens of 40 - 52cm were poorly represented. It thus appears that they are not as abundant in smaller estuarine systems and this is certainly true of Richards Bay where they would have been caught in the large mesh gill nets had they been present. An interesting feature is the relatively greater abundance of intermediate sized fish of 16 - 24cm. This might arise from easier and hence greater interchange of individuals between the smaller lagoon systems and the inshore marine environment.

(iii) Marine inshore environment

The catch consists primarily of adult fish, with the length classes between 32 - 64cm being the most abundant. Comparison with the St. Lucia catch reveals that it is specimens in the middle of this range which make up the bulk of the annual 'run' into that area. From the composition of the marine and estuarine samples it is also apparent that the largest length classes tend to be exclusively marine and do not venture into estuarine systems.

Rhabdosargus sarba

(i) St. Lucia lake system

The catch included specimens from the smallest length class of 0 - 4cm to that of 44 - 48cm; juveniles of 4 - 16cm and adults of 28 - 44cm being most abundant (Fig.13). Routine and exploratory netting failed to reveal the presence of large numbers of intermediate sized specimens and since they are subject to capture in the 5cm and 7cm gill nets (Fig.14), this length range is considered less common in the system.

(ii) Other Natal estuaries

A similar overall length range was recorded to that in St. Lucia but the catch composition differed markedly because the intermediate length classes (16 - 32cm) were extremely abundant (Fig.13). It is significant that most of these were netted in Durban Bay which is not a true estuary (see Section 3). As free interchange between the Bay and the nearby marine environment can take place the possibility arises that these fish are actually part of the marine inshore population. Evidence supporting this proposal is provided by the overlap between the length range of this group and the lower end of the marine sample (angler's catches), as well as by their scarcity in samples netted in true estuarine systems such as St. Lucia and Richards Bay. In the latter and in Natal's smaller estuaries the population seems to consist primarily of small specimens of up to 20cm, large individuals being relatively less abundant than in St. Lucia lake.

(iii) Marine inshore environment

A considerable proportion of the catch consists of specimens of 28 - 44cm and hence overlaps with the adult length range found to be abundant in St. Lucia. However the marine sample also included large adult fish of 48 - 72cm, which unlike the length classes mentioned above, have not been recorded in estuaries and therefore can be considered exclusively marine in Natal waters.

Rhabdosargus holubi

(i) St. Lucia lake system

Small specimens of up to 12cm dominated the catch and larger length classes were very poorly represented despite being subject to capture in the 5cm and 7cm gill nets (Fig.14). From this figure it is apparent that the total catch in these gill nets at all localities only amounted to 37 specimens and that the seine nets used at Richards and Durban Bays only caught 67 fish. Seen against the total catch of 2492 specimens in the juvenile sampling gear, it seems reasonable to conclude that the dominance of small specimens in the sample arises from their predominance in the populations in St. Lucia and other estuaries.

(ii) Other Natal estuaries

An essentially similar reduction in abundance with size was recorded, the main departure from the pattern of the St. Lucia catch being the greater abundance of the 0 - 4cm length class.

(iii) Marine environment

The most striking feature of this catch is that it consists largely of the adult length classes that were so poorly represented in estuaries. It also includes specimens larger than 32cm that have not been sampled in estuaries and which therefore appear to be exclusively marine in the Natal region, where they extend down to at least 40m.

Acanthopagrus berda

(i) St. Lucia lake system

Small specimens of 4 - 16cm constitute the bulk of the catch, the smallest length class of 0 - 4cm being poorly represented. Larger fish between 16 - 36cm make up a fairly constant but small proportion of the catch despite falling within the selectivity range of the 5cm, 7cm and 9cm gill nets (Fig.14) and consequently being subject to extensive netting effort. Thus the dominance of small specimens in the sample is believed to arise from a lake population structure in which juveniles greatly exceed the number of adults.

(ii) Other Natal estuaries

The catch is also dominated by small specimens but in this case the 0 - 4cm length class is very well represented. This is considered a feature of the population since these fry were mainly caught in the drag and juvenile seine nets which were used at all localities. The lower proportion of 8 - 12cm specimens than in the St. Lucia sample is at least partly due to sampling bias as they are very susceptible to capture in the shrimp trawl which was not used in other estuaries. Despite being subject to capture in seine nets adult fish make up a small proportion of the sample and their status in the population seems similar to that in St. Lucia.

(iii) Marine inshore environment

Very little is known about the marine phase of the life cycle of this species. Only eight specimens were examined during the course of sampling of shore anglers' catches and the species therefore appears to be rare in the surf zone.

Liza macrolepis

(i) St. Lucia lake system

The catch reveals that juveniles are extremely abundant and that adults up to about 36cm are common. The lower abundance of 0 - 4cm fry is considered a true population effect since they were caught in large numbers in other estuaries in the same gear as was used in St. Lucia (see Fig.14).

(ii) Other Natal estuaries

Juveniles are extremely abundant, particularly the 0 - 4cm length class which obviously migrates into these estuaries at a very early stage of life. Adults of 24 - 32cm are fairly common but fish of 12 - 24cm were caught in small numbers. Comparison with the St. Lucia catch, in which they were better represented, suggests that a reduction in the population is at least partly responsible for their poor representation in this sample.

(iii) Marine inshore environment

Adults in spawning condition occur in the vicinity of estuary mouths (see Section 7a).

Liza dumerili

(i) St. Lucia lake system

The sample does not provide evidence of any marked changes in abundance with size. However, the 0 - 4cm length class is not found in the lake and its abundance in the sample results from good catches on two incoming tides within a kilometre of the estuary mouth.

(ii) Other Natal estuaries

The absence of the 0 - 4cm length class from this catch confirms that such small specimens do not generally occur in Natal estuaries. It would appear that they occur close inshore and can be washed into estuary mouths on occasions. Larger specimens have a similar pattern of occurrence to that in the St. Lucia system.

(iii) Marine inshore environment

Adults in spawning condition occur in the vicinity of estuary mouths (see Section 7.2.2.1).

Argyrosomus hololepidotus

(i) St. Lucia lake system

An exceedingly wide length range inclusive of the 5 - 10cm and 120 - 125cm length classes has been recorded. Small specimens of 5 - 20cm were most abundant and were caught in the shrimp trawl and small mesh gill nets in the deeper parts of the lake. Specimens of 20 - 45cm were less common than larger fish of about 45 - 95cm but it is not known whether this is true of the population. Fish of 105 - 125cm were sampled in small numbers while only a few very large specimens (200, 201, 202 and 239cm) have been recorded.

(ii) Other Natal estuaries

The catch includes a smaller overall length range than that of St. Lucia and reveals that large specimens are less common in these smaller estuarine systems. Juveniles of 10 - 20cm are poorly represented but this is likely to be a sampling artifact as these length classes were mostly caught in the shrimp trawl at St. Lucia and this gear was not used in other estuaries. It seems reasonable, therefore, to consider fish of 10 - 20cm as well as those of 20 - 60cm to be abundant in these estuarine systems.

(iii) Marine environment

Although the number of specimens in this sample is small (N=146) compared with the total estuarine catch (N=3194), it includes both juveniles and adults and covers essentially the same length range. Juveniles from about 10cm are caught by shore anglers and are also trawled on the Tugela banks at depths of 30 - 40m. As they appear to be fairly widespread at sea this species may in large measure be independent of the estuarine environment during its juvenile phase of life. The larger length classes are taken from the shore and by ski-boat fishermen in depths of 60 - 70m, where they are reported to be somewhat more common in the Tugela area. The species thus has a wide distribution in Natal waters.

Elops machnata

(i) St. Lucia lake system

The catch covered a wide length range inclusive of the 5 - 10cm and 100 - 105cm length classes. Juveniles of 10 - 20cm and large fish of about 55 - 80cm were most abundant in the sample.

(ii) Other Natal estuaries

A smaller overall length range was recorded. Fish of 5 - 30cm were not obtained despite the use of the same small mesh nets as at St. Lucia and these length classes are therefore considered rare. Similarly, fish of more than 70cm formed a small proportion of the catch. This evidence suggests that the species is most abundant in the length range 35 - 70cm.

(iii) Marine environment

The sample is too small to provide an indication of the marine length composition. However, as three out of 15 fish exceeded 90cm, large adults might be more abundant at sea than in estuaries.

Miscellaneous species

The length composition of estuarine and marine samples of these species, together with estimates of their relative abundance in estuaries and comments on their distribution, are summarised in Table 3b.

5.4 Discussion

Estuarine sampling has shown that in many species juveniles greatly exceed the number of adults that occur in estuaries. Examples are: Acanthopagrus berda, Valamugil buchanani, Mugil cephalus, Liza macrolepis, Pomadasys commersonni, Pomadasys hasta, Rhabdosargus sarba and Rhabdosargus holubi. In other important species juveniles do not appear to predominate to quite the same extent but are nevertheless extremely abundant; examples being Argyrosomus hololepidotus, Elops machnata, Leiognathus equulus, Liza dumerili and Therapon jarbua. It is also interesting to record that in a number of species which are less common in Natal estuaries it is again the juvenile stages which occur with the greatest frequency. These include the kingfish Caranx ignobilis and Caranx sexfasciatus, the pouter Gerres acinaces and the snapper Lutjanus fulviflamma. It is in a minority of species that adults appear to exceed juveniles in abundance (e.g. Gerres oyena, Hilsa kelee, Johnius belengerii and Platycephalus indicus); while only adults have been recorded in the case of Muraenesox cinereus and Otolithes ruber. Thus the overall impression gained from the composition of the estuarine catch is that juvenile stages predominate.

An interesting feature of the length composition of a number of species is the rapid decline in the catch of juveniles as size increases (Fig.13, Table 3b). The most likely factors responsible for this are mortality within the estuarine environment and emigration from it. No estimates of mortality have been made in the present programme, but the work of Blaber (1973b) on juvenile R. holubi in a closed South African estuary, together with his review of literature on the subject, reveal how severe this can be. A reduction from 55 000 to 11 000 juveniles was recorded over a seven month period, an overall mortality of the order of 80% and a monthly mortality of about 30%. This was found to be of a similar magnitude to mortalities reported for other benthic fish and in most cases predation was considered to be the main cause. This was concluded to be the case in Blaber's study area where piscivorous birds appeared to be responsible as predatory fish were few in number. The shallowness of the water (2 - 5m) was considered to facilitate this form of predation as the whole estuary was fishable by the birds.

Natal's estuaries are predominantly shallow systems, piscivorous birds abound and so do predatory fish such as A. hololepidotus and E. machnata. Thus there seems every reason to suppose that R. holubi juveniles will be subject to similar mortality and that this factor was largely responsible for the recorded reduction in catch with increase in size. As an essentially similar pattern was recorded for other species such as A. berda, L. macrolepis, P. commersonni and R. sarba, it appears that the results of the present programme complement Blaber's findings and that mortality plays a very important role in the dynamics of juvenile estuarine populations.

The estuaries in which sampling was conducted in Natal are open systems so that emigration to sea is also likely to have played a role in the decline in numbers of juveniles. Although little is known about such migrations, interesting background information has emerged from studies of reproduction which have provided estimates of size at sexual maturity and have shown that most species spawn at sea. Comparison of lengths of attainment of sexual maturity with the length classes of low abundance in the St. Lucia system, shows that in a number of species it is the adolescent stage of the life cycle which is poorly represented (see below). There is thus circumstantial evidence that emigration to sea in preparation for the adult phase of life is partly responsible for the decline in estuarine abundance.

Species	Length range (cm) poorly represented in the St. Lucia system*	Length(cm) of attainment of sexual maturity+
P. commersonni	18-38	27-35
R. sarba	18-26	21-25
R. holubi	14 upwards	17-21
A. berda	18 upwards	15-21

* details in Fig.13

\+ details in Fig.35 and Table 10.

The general pattern is for some adults to return to estuaries. Evidence of this is provided by an increase in the proportion of adults in estuarine catches of species such as *A. hololepidotus*, *J. belengerii*, *P. indicus*, *P. commersonni* and *R. sarba*. The seasonality of some of these inward migrations and their relation to the reproductive cycle are considered in Sections 6 and 7.

In the case of *R. holubi* the catch composition reveals a marked tendency for the life cycle to be separated into juvenile/estuarine and adult/marine phases. This is in keeping with the pattern of occurrence reported by Blaber (1973a) for the Eastern Cape region.

To complete this general review of the length composition of the fish fauna in Natal estuaries it is necessary to mention a group of species which are represented throughout their length ranges due to the fact that they spawn under estuarine conditions. These are all species of small size and only *Ambassis natalensis*, *Gilchristella aestuarius* and *Hyporhamphus knysnaensis* have been shown to fall in this group (Section 7.2.2.3), although there may be a few others as well.

Some variation in the length composition of the populations in the different estuarine systems was recorded. In general the St. Lucia population tended to include fewer specimens in the very small length classes (e.g. A. berda, L. macrolepis and R. holubi) and a greater proportion of large adult fish (e.g. A. hololepidotus, M. cephalus, P. commersonni and R. sarba), than the populations sampled in the smaller estuaries. These features are considered to arise from the fact that St. Lucia lake is separated from the sea by the 21km of the Narrows. Thus a time lag can be expected before the very smallest fry reach the lake; while movement of adults back to sea is more likely to depend upon some motivating biological purpose than in small systems where movements with the tides seem to take place. In cases where motivation is weak or where some difficulty is experienced in orientating seawards, more prolonged sojourns are likely in this large system. In St. Lucia there also seems to be a clearer distinction between the juvenile and adult stages than in the smaller systems where intermediate length classes are better represented (e.g. A. hololepidotus, P. commersonni and R. sarba). This is likely to be attributable to the closer proximity of the latter to the sea and hence easier exchange with the marine environment.

Marine sampling has provided information on the length composition of so-called 'estuarine' species during the marine phase of their lives. As spawning is at sea the planktonic stages occur in this environment and the extent of recruitment into estuaries proves that very large numbers of juveniles must be present in the inshore zone at certain times of the year. Unfortunately, marine sampling of juveniles is difficult and facilities for this have been poor so that in most species the extent of occurrence of juveniles at sea remains a gap in the knowledge of these life histories.

Sampling has shown, however, that adults of a number of species are abundant in local waters and that these larger fish tend to favour the marine environment, some of the biggest length classes being exclusively marine. The clearest evidence for this was obtained in R. sarba and P. commersonni, for which marine inshore sampling can be considered good because 956 and 613 specimens of each were examined from the Natal coast and from Inhaca Island (Delagoa Bay). The experience gained in the course of sampling showed beyond doubt that adults occur in much greater numbers at sea than in estuaries and that this phase of the life cycles is predominantly marine. There is evidence that this also applies to species such as A. hololepidotus, E. machnata, R. holubi and T. jarbua and it is likely to be true of the adults of many other 'estuarine' species as well.

Marine sampling has provided some insight into the ichthyo-relationships between the estuarine and marine environments. As would be expected there is a close link between open estuaries and the inshore inter- and subtidal zones with which they are confluent. Comparison of catch length compositions from Natal's smaller estuaries and the inshore zone has already provided evidence of interchange between these environments. Examination of shore and skiboat anglers' catches has further emphasised this link by showing that species such as E. machnata, Hypacanthus amia, P. commersonni and R. sarba occur predominantly close inshore and are therefore seldom remote from estuarine systems. Other species such as A. hololepidotus, P. hasta and R. holubi are caught in this zone but also occur in deeper water down to 70m, thus revealing a link between estuaries and moderate depths on the continental shelf.

There is also a link between estuarine populations and those inhabiting shallow parts of the continental shelf at depths of 30 - 40m (Table 3b). Trawling on the

Tugela Bank and on a small ground off St. Lucia mouth has shown that the following species are present in these areas as well as in Natal estuaries: juvenile A. hololepidotus, J. belengerii, L. equulus, M. cinereus, O. ruber, P. hasta, Solea bleekeri and T. jarbua. Trawl catches in the protected shallows of Delagoa Bay (4 - 10m) also include Hilsa kelee and Thryssa vitrirostris, species that have been recorded in Natal's estuaries and presumably occur in shallow parts of its continental shelf as well.

5.5 Summary and Conclusion

(1) In general, juvenile fishes are much more abundant in estuaries that adults.

(2) Catches decline rapidly as the size of juveniles increases. This appears to be largely attributable to mortality caused by bird and fish predation.

(3) Adolescent fish are poorly represented in estuarine catches and this is partly due to emigration to sea in preparation for the adult reproductive phase of life.

(4) Adult populations tend to occur mainly at sea, only a relatively small proportion returning to estuaries. In some species the largest length classes are exclusively marine.

(5) The distinction between the juvenile and adult phases of the life cycle is more marked in the large St. Lucia lake system than in smaller estuaries where interchange with the sea takes place more easily.

(6) A few species occur in estuaries throughout their lives as they spawn in this environment.

(7) Most estuarine fish are inshore and shallow-water continental shelf species.

(8) The abundance of juveniles in estuaries, and the absence of positive evidence of their widespread occurrence at sea, leads to the conclusion that the most important function of estuaries in the biology

of these species is the provision of a nursery habitat for juveniles.

6. SEASONAL ABUNDANCE AND MIGRATIONS

6.1 Introduction

The object of this study has been to describe changes in abundance in the estuarine and inshore environments and from these changes to deduce as much as possible about fish migrations. The results have been related to other aspects of fish biology such as reproduction and feeding, as well as to changes in environmental conditions.

6.2 Methods

All fish movements between the sea and St. Lucia lake take place through a single channel formed by the Narrows and the estuary (Fig.3) (hereafter simply called the estuary). Changes in abundance in the estuary therefore tend to be associated with migrations and were monitored by means of a monthly gill netting programme (details outlined in Section 3.4). Quantitative estimates of these changes in abundance were obtained by comparing gill net catch rates expressed in terms of the number of fish caught per 24 net hours. These data were complemented by those obtained from routine monthly gill netting in St. Lucia south lake. Additional information on the estuarine phase was obtained as a result of sampling in other Natal estuaries, particularly Richards Bay.

Changes in seasonal abundance in the marine environment were not so easily followed and it has not been possible to obtain a strictly quantitative measure of abundance. However, the number of fish examined each month during the course of beach patrols (see Section 3.4) was much higher when the fish were abundant inshore than when they were scarce, with the result that a general indication of seasonal abundance has been obtained.

Some insight into seasonal changes in anglers' catches over a wider area of the East Coast was obtained by extracting information from reports by angling correspondents in South African newspapers. Representative coverage was ensured by subscribing to a national press cutting agency.

Unfortunately, limitations in time and personnel precluded the undertaking of a tagging programme within the present project. Consequently comments on fish migrations can only be based on recorded changes in abundance or occurrence at different localities. Nevertheless this represents an attempt to interpret the data obtained and to contribute to a better understanding of the movements that take place between the estuarine and marine environments.

6.3 Results

Migration between the lake and the sea is obviously influenced by the state of the estuary mouth. During most of the study period this remained open and in fair condition, but in 1970 it became seriously restricted towards the end of May and was closed from 11th June to 29th August. After being dredged open its cross section remained small as there was little natural scour action. As a consequence of these events the results do not reflect natural changes in abundance over two complete annual cycles. Although this is regrettable, the disadvantages have to a large extent been compensated for by the fact that during the period of closure it was possible to attribute increases in abundance in the estuary to seaward movement from the lake, whereas under normal conditions these could have arisen from movement in either direction (details in text).

Mugil cephalus

In addition to the quantitative methods already described for the determination of seasonal abundance, the presence of adult specimens of this species can be detected in shallow estuaries such as St. Lucia by the fact that they evade boats by swimming vigorously at the water surface and by leaping from it. Identification does not present a problem as the other mullet species do not attain such a large size. Visual observations thus assist in establishing the presence of this species in an area and in following its movements.

(i) St. Lucia lake system

The text below deals with the occurrence of M. cephalus in different parts of the system and presents evidence to show that it undertakes an annual seaward migration.

In the lake north of Fanies Island gill netting was conducted at irregular intervals but catches (Table 4) and sightings (Table 5) reveal that the species is present throughout the year. Specimens covering a wide length range (8.6 - 67.0cm) were netted and the good catches of small mullet in the 5cm and 7cm gill nets (asterisks in Fig.15) suggest that the area supports a large population of juveniles.

In the south lake catches in these nets were very poor throughout the study period (Fig.15) and juveniles are consequently considered to have a preference for the northern parts of the system. However catches in the 9cm and 13cm nets show that sexually mature specimens were seasonally abundant. No fish were netted from October 1968 to February 1969, but in March a sudden increase occurred and was followed by a period of abundance which terminated in July. From then until December very few mullet were netted. In 1970 shoals appeared somewhat earlier but the period of abundance again terminated in July. (Possible reasons for the short term reductions in catch during their periods of abundance are discussed in Annexure A, pages 5 and 10-12). A notable difference between the two years was the large number of mullet in the south lake during September 1970 which were trapped in the system by the closure of the St. Lucia mouth. In October, catches dropped markedly as a result of movement out to sea after the mouth was reopened but it is possible that many mullet did not leave the lake and that this accounts for the good catches recorded in December 1970.

In the estuary gill netting reveals a pattern of occurrence similar to that in the south lake (Fig.15). Despite extensive sampling with the 5cm (1253 hours) and 7cm nets (766 hours) very few small mullet were caught and they can therefore be considered rare in this area. Catches in the 9cm and 13cm nets again show marked seasonality. Mullet were absent from August 1968 to March 1969 and were first netted in April, a month after they appeared in the south lake. Catches increased to a peak in June, dropped in July and the last specimens were netted in September. None were sampled in October or during the summer of 1969/70, as was the case the previous year. The cycle of abundance during 1970 differed considerably from that of 1969 but the variations can be correlated with abnormal environmental conditions. Mullet were first netted in May, a month later than in 1969 and four months after they first appeared in the south lake. This delay might have resulted from difficulty being experienced in finding the exit from the lake due to the exceptionally low lake levels prevalent at the time (this possibility is considered in more detail in Annexure A, p.6). During June catches increased and remained good until September, after which a sudden decrease occurred. This extension of the period of abundance was caused by the closure of the estuary mouth.

Sufficient information has been obtained from the gill net catches and visual observations reported above for the distribution of mullet shoals in St. Lucia and the seaward migration of this species to be described in some detail. During the summer months of 1968/69 and 1969/70 shoaling activity of juvenile, adolescent and adult specimens intensified in the north lake and a general southward movement took place. However, the migratory urge amongst the sexually immature stages was apparently not as strong as for adults because shoals of these smaller specimens were not observed south of Fanies Island and they were not netted in the south lake. The arrival of adult fish in this area has already been described and gill net catches (Fig.15) show that this took place 1 - 3 months before the increase in abundance was recorded in the estuary. Visual observations revealed beyond doubt that mullet shoals moved out of the lake by moving down the Narrows and towards the sea. This was partly responsible for the increase in abundance of the species in St. Lucia estuary. Study of the reproductive cycle (Section 7.2) has shown that this is a spawning migration and that few mullet return to the lake after breeding at sea.

A more detailed account of these two annual migrations is provided by Wallace (1974; Annexure A). In this paper the movements of the shoals are related to the unusual hydrological and topographical features of the St. Lucia system and possible mechanisms involved in their seaward orientation are discussed. Although the roles of steep salinity gradients and gross salinity changes are not discounted, it is suggested that organic cues derived from sea water inflow and freshwater drainage might also serve an orientation function.

An interesting aspect of the winter abundance of <u>M. cephalus</u> in St. Lucia estuary is that the fish are derived from both the lake and the sea. Their arrival in the estuary is dramatic because they leap clear of the water for no apparent reason and literally hundreds jump into the air simultaneously when they are harried by sharks or disturbed by boats. Records kept by conservation personnel of the Natal Parks Board show that they are remarkably consistent in their dates of arrival:

Year	Date of Arrival
1968	25 April
1969	12 May
1970	4 May
1971	7 May
1972	12 April
1973	23 April
1974	17 April

It is alleged that the marine shoals arrive before the lake mullet reach the estuary. In 1973 the movement of the lake fish was kept under close scrutiny and showed that the migration down the Narrows started on 30th April, thus confirming that at least on this occasion this contention was correct.

(ii) Other Natal estuaries

Catches of adult specimens in Richards Bay (Fig.15) show a similar pattern of abundance to St. Lucia, while catches in Durban Bay and in other smaller estuarine systems indicate that mullet move in and out of river mouths with the tides, apparently remaining in the larger estuarine lagoons for somewhat longer periods. This behaviour continues until about August.

(iii) Marine Environment

During winter great concentrations of *M. cephalus* occur over the continental shelf in the St. Lucia area and the species is abundant inshore along most of the Natal coast. However it is not known where these shoals come from or where the species occurs during the non-breeding season.

Pomadasys commersonni

(i) St. Lucia lake system

During the winter months very few grunter are caught by anglers but with the advent of spring and early summer the fish arrive at the estuary in great abundance and literally thousands of fishermen flock to the area to take advantage of the annual 'run'. Large shoals move in and out the mouth and Narrows with the tides and there is also a migration into the lake where angling improves accordingly.

Gill net catches reflect these changes in seasonal occurrence. Catches in the estuary (Fig.16) indicate that the species was abundant in August 1968 and although catches were considerably lower in August 1969, it is clear that this month marked the start of the period of increased abundance. In 1970 the mouth was closed from 11 June to 29 August, but the capture of grunter from adjacent beaches and their reappearance in gill net catches in September, suggest that the species would have entered the estuary during August had this been physically possible. The small cross section of the mouth after it was re-opened is likely to have been partly responsible for the poor catches during September, October and November, 1970.

Gill net catches in the south lake indicate that the seasonal occurrence in this part of the system is similar to that in the estuary.

Evidence is presented in Section 7.2 to show that the fish which migrate into the St. Lucia system are in post-spawning condition.

The duration of estuarine abundance is variable. Catches in the estuary declined to a low level in February 1969 but in the following year this took place later and the species was still relatively common in May. It is clear, however, that the period of lowest occurrence is during winter and since this applies to both the lake and estuary the reduction in the population can be attributed to emigration to sea. Although no grunter were netted in the lake in April, May or June 1969 catches during the winter of

1970 prove that some adults remain in the system.

(ii) Marine inshore environment

Catches in the Durban area show a seasonal trend in occurrence (Fig. 17), the species being more abundant during spring and summer than in autumn and winter. This pattern is essentially similar to that recorded at St. Lucia. An interesting difference is that in the Durban area the increase in abundance takes place in September (1972 and 1973 data), whereas in St. Lucia estuary this was recorded in August. Since the fish move into the estuary from the sea, the possibility is raised that the inshore increase takes place earlier in the north and that there is a southward movement of shoals. Caution must, however, be exercised in advancing any theory of longshore migration because onshore movement from slightly deeper water could account for the increased abundance in the inshore environment.

Rhabdosargus sarba

(i) St. Lucia lake system

This species has been recorded in the south lake throughout the year and no seasonal trend in occurrence has been detected.

In the estuary catches were erratic and do not reveal any clear cycle of seasonal abundance (Fig.16) or correlation with salinity conditions in the north lake. The generally low catch rates indicate that the species occurred in the estuary in relatively small numbers during most of the study period. The gonad condition (post spawning) of these fish shows that an inward migration is likely to occur between June and November and provides a possible explanation for the occurrence of the species in the area throughout the year (see details in Section 7.2).

(ii) Marine inshore environment

Research samples (Fig.18) indicate that this species is present throughout the year and that its period of greatest abundance extends from about May to November.

Argyrosomus hololepidotus

(i) St. Lucia lake system

The species has been recorded in the south lake throughout the year but there is no evidence of seasonality. This is because its occurrence has been influenced by salinity levels in the northern parts of the system, high salinities being associated with a southward movement of fish (see Fig.12, Section 4.3).

In the estuary catches in the 9cm gill net reveal the presence of specimens within its selectivity range (35 - 75cm) throughout the year (Fig.16). Slightly increased catches were recorded in April 1969 and in May and November 1970, but on the basis of the data obtained no conclusions can be drawn concerning seasonality within this length range. In contrast, the catch of larger fish in the 13cm gill net (55 - 100cm total length) reveals a repeated trend in seasonal occurrence. Increased catches were recorded in April/May 1969 and in May 1970, as well as from August to October (1968 and 1969) and in August/September 1970. During the interim periods catch rates were low.

In the absence of tagging studies evidence of directions of movement through the Narrows can only be circumstantial. However some movement into the lake must occur during the period June to November because it is during these months that spent specimens are recorded in the Narrows and also appear in the lake (see Section 7.2). Whether movements back to sea also take place during these months is unknown.

(ii) Marine inshore environment

Research samples (Fig.25, Section 7.2) and reports of anglers' catches indicate that the species occurs throughout the year on the Natal coast but that it is more common during the cooler months. Small specimens (2 - 5kg), known to anglers as 'shoal salmon', increase in abundance in April and generally seem to precede the increase in adults (mainly 20 - 40kg and known as 'dagas') by about a month. The sequence of increase in abundance, which starts to the south of Natal and moves up the coast with time, has led to the generally held belief that there is a north-eastward movement along the coast during autumn and winter. As the decline in abundance follows the reverse pattern a return migration is believed to occur during spring and early summer. Careful questioning of commercial lineboat fishermen that operate in Natal waters has indicated that this species is only caught in small numbers offshore. It therefore seems unlikely that the winter abundance arises from inshore movement of local fish and the longshore migration theory can be accepted.

Acanthopagrus berda

St. Lucia estuary

This species has not been caught in large numbers but it does occur seasonally (Fig.16). Catches increased during the months March to June 1969 and again from May to July 1970. These months fall within the spawning season.

Liza macrolepis

St. Lucia lake system

Catches in the south lake (Fig.16) were good during the period June to August 1969, while in 1970 they

they showed an increase in June and were again good in July and August. During the interim periods very few species were netted. In the estuary good catches were made from August to November 1969 (the drop in October is attributable to adverse weather conditions during the sampling period), but in 1970 the natural cycle of abundance was influenced by the variable condition of the estuary mouth and good catches were restricted to July and August.

In 1969 the lag in peak occurrence between the lake and estuary could have arisen from migration from the lake towards the sea, or vice versa. However catches during the 1970 period of mouth closure provide some insight into the movements that take place. Although the fish netted in the estuary in March, April and May could have entered the area from the sea, the catch rate during these months was low compared with that of July and August when such a migration was impossible. It therefore seems reasonable to propose that the increase in July and August resulted from seaward movement of fish from the south lake and that this continued after the mouth was re-opened and accounted for the dramatic drop in catch in both the lake and estuary. According to this interpretation of the data the seasonal occurrence of the species in the south lake would arise from the passage of shoals through this area on their way to sea.

Evidence obtained from the study of the reproductive cycle indicates that spawning takes place at sea and that both pre- and post-spawning fish occur in the lake (Section 7.2). There must therefore be a seaward migration of pre-spawners (as suggested above) and a movement of spent fish back into the lake.

Liza dumerili

St. Lucia estuary

The occurrence of this species is markedly seasonal (Fig.16). An increase in catch was recorded in July 1969 and good catches were made from August to November (the drop in October is attributable to adverse weather conditions during the sampling period). Hardly any fish were obtained from December 1969 to May 1970, but catches increased again in July and August when the estuary mouth was closed and the fish must therefore have come from the lake. After the mouth was re-opened catches dropped markedly but the catch in November shows that some fish were still in the vicinity. The data obtained in 1969 and 1970 thus indicate that this species occurs with increased abundance from July to November.

Reproduction studies confirm that pre-spawning specimens move out to sea but show that post-spawners also move back into the lake (Section 7.2).

6.4 Discussion

In the life cycles of most species the first migration which is undertaken is the movement of fry from the sea into estuaries. Once this has occurred considerable periods tend to be spent in this environment and some species only return to sea with the approach of adolescence (details in Section 5.4). Some examples are given below.

In the St. Lucia system a decline in abundance of *P. commersonni* that is partly attributable to emigration to sea is evident by the time the species attains a length of 16 - 20cm (Fig.13). According to estimates of juvenile growth rate (Section 8.3.2) this takes place about a year after the fry entered the system. A similar estimate of the growth rate of juvenile *R. sarba* indicates that this species is likely to be about a year old when it starts moving back to sea. Research by Blaber (1973a) on the growth of juvenile *R. holubi* shows that in the warm-temperate Kleinemond estuary the average summer growth increment is about 10mm per month and that this drops to about 3.5mm during the winter; growth in the first year thus presumably being of the order of 80mm. Since winter temperatures are not as low in the sub-tropical St. Lucia system a faster winter growth rate can be expected and the decline in abundance of this species at lengths of about 100mm is thus also likely to involve specimens that are about a year old.

In contrast, *M. cephalus* spends a considerably longer period in the lake before it returns to sea. This occurs at lengths from 40cm upwards (mostly 48 - 58cm) by which time it is already sexually mature. As its length at maturity (Section 7.3) and growth rate during the first year of life (Section 8.3.2) in Natal are similar to east and west Australia (Kestevan, 1942; Thomson, 1951) and to eastern Florida (Jacot, 1920; Hubbs, 1921), it seems reasonable to apply the length-for-age estimates of these workers to local *M. cephalus*. This shows that the specimens that migrate out of St. Lucia are likely to be three to four years of age. Since there is very little movement of adults back into the lake (Section 6.3), it is apparent that the species spends a significant part of its life in the system before migrating seawards.

In Natal's smaller estuaries there tends not to be such a clear distinction between the juvenile and adult stages in the life cycles and intermediate length classes are better represented than in St. Lucia (details in Section 5.4). This is attributed to the proximity of these small systems to the sea and to easier movement between the estuarine and marine environments. Consequently juveniles might not spend such long uninterrupted periods in these smaller systems, but after moving out to sea can more easily return again.

Once sexual maturity has been attained migrations and changes in seasonal abundance are likely to take place in response to spawning activity. It is therefore interesting to relate the results of the present study to those obtained from the investigation of areas and seasons of spawning. Details of the latter are presented in Section 7.2 but to facilitate the discussion that follows the salient facts have been summarised in Table 6. From this it is apparent that in a number of species the periods of abundance in the inshore and estuarine environments are essentially similar and tend to be associated with spawning. Thus in species such as A. berda, M. cephalus, L. macrolepis and L. dumerili the migrations that take place involve fish in immediately pre- and post-spawning condition. All three of the mullet species mentioned above migrate from St. Lucia lake to spawn at sea and with the exception of M. cephalus, return to the lake after spawning. The period of estuarine abundance of the spotted grunter, P. commersonni, also coincides with the inshore spawning season but most specimens that enter St. Lucia estuary are in post-spawning condition and this is particularly true of those that migrate into the lake. In the case of the Natal stumpnose (R. sarba) the period of inshore abundance also coincides with the spawning and post-spawning phases of the reproductive cycle but it does not undertake such a marked post-spawning migration into St. Lucia lake. Most specimens of this species are reproductively inactive when they move between the sea and the lake; and this is true also of the kob A. hololepidotus. This utilisation of estuaries by adult fish is likely to be in response to the rich feeding regime typical of these areas.

An interesting fact associated with the congregation of shoals inshore is that there are obviously far greater numbers of fish involved than can be accounted for by emigration from Natal estuaries. An example is M. cephalus which occurs seasonally in vast numbers in the surf zone from northern Zululand to at least as far south as Durban. It is also true of P. commersonni which only occurs in estuaries in limited numbers during the winter months but which appears inshore in abundance from August/September onwards. There must therefore be a tendency for marine shoals to move into the Natal inshore environment during these times of the year and the question arises as to where they come from.

Unfortunately very little is known about the movements that take place at sea because no tagging programme has been conducted on this group of fishes. Any consideration of the question posed above can only be based on circumstantial evidence and must be somewhat speculative. This is nevertheless an interesting exercise and provides some indication of the migrations that are likely to take place.

In Section 5.4 it was shown that numerous species occur in estuaries and on the adjacent continental shelf and it was apparent that they formed continuous populations. Movements between these environments can be expected during the course of the life cycles and it seems reasonable to suggest that adults from estuaries congregate with adults already at sea during the spawning season. In cases where spawning occurs in the shallow inshore waters an increase in abundance could be expected to result from emigration from estuaries and from an inshore movement of marine shoals. This is considered likely to be at least partly responsible for the seasonal inshore increase in abundance of species such as M. cephalus, L. macrolepis, L. dumerili, A. berda, R. sarba and P. commersonni.

In essence the theory proposed above amounts to seasonal variation in the distribution of fish that are within the Natal region. However on its own this is likely to be an oversimplification and it seems probable that longshore migrations are also responsible for the increase in abundance of certain species in Natal waters during their spawning seasons. Unfortunately in the absence of detailed factual information this cannot be substantiated.

Some information is available on the general trends of seasonal distribution along the East Coast. Longshore movements in a south westerly direction take place during summer with the result that species such as the spotted grunter (P. commersonni) extend into south coast waters. Smith (1961, p.16) records that: 'trawlers occasionally make hauls of this grunter in 20 fathoms or more'; 'trawlers have taken many tons of them in about 10 fathoms near Bird Island' (Algoa Bay); and 'In summer the spotted grunter still extends regularly as far south as Mossel Bay'. In fact this species has been recorded in False Bay (Day et al, 1970) which shows that at times it extends west of Cape Agulhas. That it has occurred in these waters over considerable periods of time is shown by Smith (1950), who reports the presence of its characteristic supraoccipital bones in Strandloper kitchen deposits in False Bay and at Hermanus which have an estimated maximum age of 3 000 years. The means whereby these fish came into the possession of primitive man is convincingly ascribed by Smith to the sudden onsets of cold water which cause temperatures to drop 8 - 10°C overnight and result in instances such as the following: 'I have known of over 200 mature fishes, up to 10lb. in weight, being picked up, dead or numbed, in a morning on such an occasion. Those were but a fraction of the total number stranded and killed'(Smith, 1950, p.781).

Other typically Natal fishes also migrate south westwards. The distribution of R. sarba is described by Smith (1942, p.548) as follows: 'Sarba has been found to extend as far south as the Bashee River; beyond that, westwards, the species is rare, but large specimens sometimes reach as far west as Mossel Bay, several generally being taken each year in the late summer at Knysna'.

Temperature clearly plays an important role in determining the distribution of these fishes. A general south-westward shift in distribution of warm water forms takes place in summer when inshore temperatures on the south coast between Port Elizabeth and Cape Agulhas rise to 19 - 21°C, which approximates the lower end of the temperature range found inshore along the Natal coast during winter (Fig.19). Sudden reductions in temperatures resulting from upwelling (Korringa, 1956) serve to limit this penetration of South Coast waters and at times are so severe as to cause mortalities (see above). However, the general trend is probably for the sub-tropical forms to retreat back in a north easterly direction as water tmperatures start to fall in autumn.

Conversely, fishes such as the kob (A. hololepidotus) and leerfish (Hypacanthus amia) which occur most commonly on the Cape coast, show a north-easterly shift in their distribution during the cooler months of the year when both become plentiful in the Natal inshore zone.

The extent to which these migrations are assisted by ocean currents is unknown. Whereas these large species of fish must be physically capable of undertaking extensive migrations and could presumably move independently along the coast as temperatures change in favour of their specific preferences, it seems likely that their movements take place in association with the currents that prevail. Thus it is probable that the south west flowing Agulhas Current facilitates movement in this direction along the whole East and South coasts, perhaps having a greater bearing on the distribution of shallow water forms such as P. commersonni and R. sarba along those parts of the coast where the continental shelf is narrow and the current close to shore.

The extent to which a return movement is assisted by a north easterly inshore counter current is unclear. However, there is considerable evidence that north easterly water movements do take place (Harris, 1961; Mallory, 1961), although they do not seem to be continuous and little is known of their seasonal variation (pers.comm. Dr. A.F. Pearce. National Physics Research Laboratory, C.S.I.R., Durban). De Decker (1973, p.191) states that to the east of Knysna 'inshore upwelling develops into the cold Counter Current, which is traceable both physically and biologically as far as Durban and beyond'. Baird (1971) has studied the possible role of the counter current in relation to the winter appearance of pilchards (Sardinops ocellata) in Natal waters (the so-called Natal 'sardine run'). His analysis of synoptic sea surface temperature charts during the two year period January 1969 to October 1970 revealed the presence of an inshore tongue of cold water which extended with only slight interruptions from the south western Cape to just south of St. Lucia during June and July of both years. This contrasted with the situation in all other months when the cold water fluctuated between Cape Agulhas and the Bashee River. On this basis Baird postulated that the flow of the counter current provides the means for the movement of sardines into Natal waters during winter.

In the opinion of the present author, the changes which take place in the ichthyofauna of Natal during winter as a result of a north-easterly shift in distribution of typically Cape fishes, is of such a general nature as to provide strong evidence for the existence of inshore current transport.

6.5 Summary and Conclusions

(1) The first migration undertaken by most species is the movement of fry from the sea into estuaries.

(2) Species such as P. commersonni, R. sarba and R. holubi start to return to sea after about a year, at which stage they are still sexually immature.

(3) <u>M. cephalus</u> remains in the St. Lucia system for an estimated 3 - 4 years before sexually mature adults undergo a seaward spawning migration.

(4) Although it is possible that the 1969 and 1970 migrations of this species were assisted by steep salinity gradients and gross salinity change, it is suggested that organic cues derived from sea water inflow and freshwater drainage also served an orientation function (Annexure A).

(5) Interchange between the sea and populations in small estuaries seems to be more frequent than in large systems such as St. Lucia.

(6) Migrations and changes in seasonal abundance of sexually mature fish tend to be associated with the spawning season and many migrants are in pre- and post-spawning condition. However some species migrate between these environments during the inactive phase of their reproductive cycles.

(7) In a number of species the period of inshore abundance coincides with the spawning season.

(8) The inshore spawning shoals appear to be formed by emigrants from estuaries and from an inshore movement of marine populations. Longshore migrations might also be partly responsible.

(9) Seasonal shifts in distribution along the East and South coasts occur and are associated with changes in water temperature. Sub-tropical East Coast species extend into South Coast waters in summer and warm temperate species enter East Coast waters during winter.

(10) It is probable that these longshore migrations are assisted by the Agulhas Current and possibly by an inshore north-flowing counter current.

7. REPRODUCTION

7.1 Introduction

Reproduction is a basic function in the biology of any species and this is equally true of an assemblage of species forming a faunistic component within an ecosystem. Consequently particular attention was paid to reproduction in the present programme and as much information as possible was collected from all the species netted during the course of routine sampling.

The investigation of areas and seasons of spawning was based upon an assessment of the condition of the gonads of fish collected from both the estuarine (Aug. 1968 - Dec. 1970) and marine environments (1972 and 1973). This also provided information on lengths of attainment of sexual maturity. Plankton netting for fish larvae was conducted in the St. Lucia system (1969 and 1970) as this formed another method of assessing whether spawning occurs under estuarine conditions.

Details of the sampling programme have already been given (Section 3.4). The results obtained are presented and discussed for each species; while the main features of the reproductive biology of the fauna as a whole form the subject of a general discussion (7.4).

7.2 Seasons and areas of spawning

7.2.1 Methods

The cycle of gonad development was divided into six stages, each of which was defined according to its main macroscopically distinctive characteristics. Males and females were assessed separately.

Due to the scope of the project it was impossible to confirm the validity of these stages histologically for each species. However this was done for *Mugil cephalus* in which microscopic evidence of gonad development verified the gross stages that had been defined. Application of these stages to estuarine species in general was thus considered justified.

The stages were defined as follows:

Females

Inactive (I)	:	Gonad small; no ova visible.
Active (A)	:	Gonad slightly enlarged, superficial blood vessels developing; distinct small ova visible.
Active-ripe (AR)	:	Gonad considerably enlarged, superficial blood vessels well developed; ova enlarged and opaque.
Ripe (R)	:	Gonad at maximum size, firm to the touch, superficial blood vessels fully developed; ova very tightly packed, opaque, not easily teased free in region of vent.
Ripe running (RR)	:	Ova translucent; if still tightly packed, fish on point of spawning, if partially suspended in fluid and stream out of vent at slightest pressure on abdomen, fish in process of spawning.
Spent (S)	:	Gonad size variable, flaccid due to evacuation, bloodshot due to haemorrhage; ova opaque.

Males

Inactive (I)	:	Gonad small, milt cannot be extruded.
Active (A)	:	Gonad slightly enlarged; some milt can be extruded under considerable pressure.
Active-ripe (AR)	:	Gonad considerably enlarged; milt viscous and creamlike, more easily extruded.
Ripe (R)	:	Gonad at maximum size, firm to the touch, white in colour; milt more fluid and milk-like, easily extruded.
Ripe running (RR)	:	Milt flows freely from vent at slightest pressure on abdomen.
Spent (S)	:	Gonad size variable, flaccid due to evacuation, pink from haemorrhage; milt can still be extruded.

These stages were applied during the phase of the study involving adult fish in the estuarine environment (August 1968 to December 1970). However during this period spent gonads in the main species were subdivided into 'early' and 'late' groups. This was done because it was felt that the definition of spent incorporated rather a wide range of gonad condition and included fish which still had enlarged gonads and appeared capable of some further spawning, as well as truly spent specimens. This distinction has been maintained in the processing of the results.

At the start of the marine phase of the study (1972) it was considered advantageous to apply this distinction to all species. The 'early spent' gonad stage has been termed 'partially spawned' and is distinguished from true spents as follows:

<u>Females</u>

Partially spawned (PS): Gonad still enlarged, with a distinct lumen, flaccid due to partial evacuation, soft to the touch, somewhat bloodshot due to haemorrhage; large number of ova still present, opaque, not tightly packed, easily teased free in region of vent.

Spent (S) : Gonad reduced in size, very bloodshot due to haemorrhage; relatively few ova remain, still visible macroscopically.

<u>Males</u>

Partially spawned (PS): Gonad still enlarged, flaccid to the touch due to partial evacuation, pink in colour due to haemorrhage; considerable quantities of milt can still be extruded.

Spent (S) : Gonad reduced in size, pink in colour; some milt still present.

The following comments should be made concerning aspects of the gonad staging technique. In the case of large sexually mature fish inactive gonads were easy to recognise, but as size decreased difficulty was experienced in distinguishing between the inactive gonads of mature fish and the undeveloped gonads of immature specimens. To avoid bias in the representation of the inactive stage of the gonad cycle, a specimen was only accepted as being truly inactive if its length exceeded that at which most specimens were estimated to be sexually mature (arrowed in Fig.35 and indicated by asterisks in Table 10).

In order to define seasons and areas of spawning it was obviously important to select suitable criteria for the identification of fish in true spawning condition. Reference to an FAO Manual of Methods in Fisheries Biology (Laevastu, 1965) indicated that immediately before spawning the ova change from being opaque to translucent in appearance. (According to de Vlaming (1972) this is due to the coalescence of yolk globules). In addition the ova become loosely suspended in the ovary and flow freely from the vent in response to slight pressure on the abdomen. In M. cephalus this has been shown to result from absorption of water by the fish (Fish Farm. int.(1), 1973). These characteristics make the identification of a female that is on the point of or in the process of spawning a relatively simple matter. In the male the criteria are not quite so definitive because milt will flow from the vent of a ripe specimen which is not yet in true spawning condition. However this tends to be a rather creamy consistency and is distinguishable from the milk-like milt which pours out of the vent of a male in true ripe running condition.

Plankton netting for fish larvae was conducted each month in St. Lucia south lake (off Charters Creek) and in the estuary within 4km of the mouth. Owing to the shallowness of these areas the net (specifications in Section 3.4) was mounted underwater near the bow of the boat where it was not subject to clogging with silt churned up by the motor. A standard technique was adopted which involved netting for 10 minutes at each locality at 'idling' speed

($\pm$ 4km/hr). This was always done at night as it was considered that larval fishes might spend the daylight hours in the benthos.

7.2.2 Results

In the main species (Section 7.2.2.1) the data for St. Lucia lake and estuary have been presented separately but the data obtained from Durban Bay, Richards Bay and other estuarine systems have been lumped. In the other species included in the study (7.2.2.2) the data from all estuarine localities have been combined.

As differing trends in gonad development were not detected between the sexes the data for male and females have been lumped.

The results are presented in the form of histograms in which the actual number of specimens in each stage of gonad development has been plotted. This was done because sample size varies in accordance with seasonality of occurrence in estuaries and there are consequently months when small samples were obtained and when it would have been misleading to express the data in terms of percentages. An advantage of plotting the actual number of specimens is that the area under the histogram is proportional to the size of the sample (Rayner, 1967). This focusses attention on the state of the gonads during the periods of estuarine abundance when relatively large samples were obtained.

7.2.2.1 Main species

Mugil cephalus

(i) St. Lucia estuary

The condition of the gonads during this species' seasonal occurrence in this area is as follows (Fig.20): Fish with developing gonads appear in April and by May/June a large proportion are in immediately pre- and post-spawning condition (gonads ripe, partially spawned and spent). This suggests that spawning takes place somewhere in the vicinity of St. Lucia estuary. However the absence of any ripe running fish in the 1969 sample, and the recording of only a single female in 1970 (May, arrowed in Fig.20) with clear ova that were still tightly packed and not yet able to flow from the vent, is evidence that the estuary is not a spawning area. The decline in abundance after September and the low incidence of inactive fish indicates that the species leaves this area after the spawning season.

In 1970 the closure of the mouth from early June to the end of August trapped large numbers of ripe mullet in the system but no spawning was detected in the Narrows where salinities of 18 - 39 ‰ were recorded (Fig.21). Instead, it became apparent that the gonads were degenerating and that their contents were being resorbed, causing a reduction in gonad size to that typical of the spent condition (represented by hatched sections superimposed on the histograms in Fig.20). Histological examination of gonads in this condition confirmed that breakdown of oocytes was taking place and that this closely followed the degenerative process described by Abraham (1963) for <u>Mugil capito</u> (Abraham's study was based on fish that had been transferred to Lake Tiberias (Sea of Galilee) for purposes of aquaculture and resorbed their gonads because they were unable to reach the sea to spawn).

(ii) <u>St. Lucia lake</u>

The data show that the gonads are mainly inactive during January, February, October, November and December. Development takes place during March, April, May and June, a large proportion of the population being in ripe condition during the latter two months (shown most clearly by the 1970 data). However no ripe running fish have been recorded in the lake and spawning is not considered to occur in this environment. During 1969 when the estuary mouth was permanently open very few partially spawned or spent fish were sampled, from which it is evident that there is not a large scale movement of post-spawners back into the lake.

Deviations from the above pattern that are attributable to the temporary closure of the mouth in 1970 are considered to be as follows: some fish with gonads in ripe condition were recorded as late as August and September. Numerous specimens showed signs of resorbing their unspawned gonadal contents (hatching in Fig.20; discussed more fully above). Many post-spawners were trapped in the system and failed to leave once the mouth was re-opened, thus accounting for the greater proportion of spent and of back to inactive fish recorded between September and December.

(iii) Other Natal estuaries

The cycles of seasonal occurrence and gonad activity are essentially the same as those described for St. Lucia estuary. When the species increases in abundance in May the gonads range from active to spent and it is thus apparent that spawning has already started. No ripe running specimens have been recorded and after the breeding season few adult specimens remain in these estuaries.

(iv) Marine environment

A small sample (N = 89) was obtained as this species is not caught by shore anglers and is difficult to net in the surf zone. However comparison of the June sample (taken in the Durban area and in northern Zululand) with similar catches in estuaries provides confirmatory evidence that this month falls within the spawning period.

(v) Discussion

Although spawning has not been recorded it is possible to infer when it takes place from the occurrence of ripe, partially spawned and spent gonads in estuarine catches. These show that spawning starts in May (Fig.20) and continues until September, but that it is probably less intense during the last two months of this period. These gonad stages indicate that spawning is likely to occur in the shallow inshore marine environment, but it possibly also extends some distance out onto the continental shelf. In local waters the breeding pattern thus seems to be somewhat similar to that described by Anderson (1958) for south east Florida, where spawning occurs close inshore in the region where the continental shelf is narrow and the Gulf Stream flows near to the coast.

It is interesting that ripe fish did not spawn in St. Lucia estuary when they became trapped by the closure of the mouth. This suggests that specific environmental conditions and perhaps even an environmental 'trigger' are needed to initiate spawning and that these requirements are not normally satisfied in open estuaries and were certainly absent in St. Lucia after the mouth closed. In fact the 'block' which the absence of suitable conditions produces is so definite that despite being on the point of spawning the mullet in St. Lucia did not shed their gonadal products, but took what would appear to be a more complicated physiological alternative and resorbed them instead. Thus the dependence upon being at sea in order to spawn is very basic to the biology of this species and possibly became established genetically in response to a selection pressure against estuarine spawning resulting from mortality of fertilised egg and larval stages in this environment.

It is interesting to compare the gonad cycle with the periods of seasonal abundance in the different sampling areas. In St. Lucia south lake *M. cephalus* is abundant from February to June (Fig.15), a period during which gonads develop from being inactive to the immediately pre-spawning ripe condition (Fig.20). It is thus clear that the seaward migration through the south lake takes place in preparation for spawning. However, the very low incidence of partially spawned and spent gonad stages reveals that there is not a comparable return migration of post-spawners into the lake.

In St. Lucia estuary and the other estuarine sampling areas the species was found to be abundant from May to July. During this period the fish are in immediately pre- and post-spawning condition.

In summary, the role of the different sampling areas in the reproductive cycle can be outlined as follows (see Fig.22): in St. Lucia lake gonad development takes place but the fish leave the area to spawn and very few return thereafter. In St. Lucia estuary the fish are primarily in immediately pre- and post-spawning condition but ripe running specimens are absent. This is also true of the other areas of estuarine sampling. Spawning takes place at sea during the months May to September.

<u>Pomadasys commersonni</u>

(i) <u>St. Lucia estuary</u>

The seasonal pattern of gonad activity which becomes apparent from the data in Fig.23 is as follows: at the start of the grunter 'run' in August gonads are mainly in a partially spawned and spent condition. During 1968 this continued to be the case until the end of the season in about December, while in 1969 the proportion of partially spawned gonads decreased in association with an increase in the proportion of spents during this period. (The 1970 data do not show the above characteristics as the 'run' did not start normally owing to the closure of the mouth. The relatively few specimens that entered the estuary from September onwards were already in spent condition). During the months January to July gonads are in a late spent and inactive condition.

Fish with maturing gonads in active, active-ripe and ripe condition are rare and it is clear that the pre-spawning phase of the reproductive cycle takes place elsewhere. As only two out of a total sample of 1189 specimens were recorded with true ripe running gonads it is highly improbable that the estuary and Narrows constitute a spawning area. However these specimens and the presence of considerable numbers of partially spawned fish capable of further spawning provide evidence that it occurs at no great distance from this area.

(ii) St. Lucia lake

It is evident that this sample conforms to the general seasonal pattern of gonad activity described above but that ripe running specimens are absent and partially spawned specimens occur less frequently. Spent and back to inactive fish make up a correspondingly increased proportion of the catch and the lake is in fact populated to a large extent by fish in the post spawning and non-breeding phases of the reproductive cycle. The virtual absence of specimens with developing gonads is a feature shared with the sample obtained in the estuary.

(iii) Other Natal estuaries

It is apparent from Fig.23 that the gonads were primarily spent or inactive and an influx of fish with partially spawned gonads (comparable to that in St. Lucia estuary) was not detected. However the presence of four partially spawned fish in October and the increase in the number of spents recorded in this month indicate that post-spawners do enter other Natal estuaries.

(iv) Marine inshore environment

The sample (N = 523) consists primarily of fish caught in the Durban area, only six specimens having been examined from other parts of Natal. The most significant fact arising from the data (Fig.23) is that spawning (ripe running) fish were recorded during the months September to December. These occur in association with a relatively high proportion of specimens in partially spawned condition which is consistent with what would be expected in a spawning area. Although only 14 ripe running fish were recorded this is likely to be because fish are in this condition for a relatively short period and are hence subject to a lower probability of capture than the other pre- and post-spawning gonad stages. It is also possible that spawning fish do not feed actively and are less susceptible to capture by anglers. Thus a low proportion of ripe running specimens in a sample can give a false impression of the extent of spawning and this is possibly true in the Durban area.

After December no ripe running and very few partially spawned specimens were recorded; while the proportion of spents decreases in favour of fish with gonads that have reverted to the inactive state. Fish with active, active-ripe and ripe gonads are virtually absent from the sample.

In addition to the above a total of 68 specimens was obtained from Inhaca Island (off Lourenco Marques, Mozambique). Comparison with the Durban catch shows that in the months for which data were obtained the gonad stages are similar at the two localities (compare Fig.23 and Table 7). The two active specimens recorded at Inhaca in April give a clue to the start of the gonad maturation phase and this is also provided by the few active fish recorded in the Durban area in May and June 1972.

(v) Discussion

Spawning has been recorded in marine samples from September to December. However the ripe running female recorded in St. Lucia estuary in August 1968, and the high proportion of partially spawned and recently spent fish during August 1968 and August 1969, indicate that spawning is already well underway by this month. Estuarine data confirm that December approximates the end of the spawning season. Thus most spawning is considered to occur during the five month period August to December. In the light of the above, the statement made by Day and Morgans (1956) that spawning takes place between November and February must be considered as only partly correct.

It is interesting to compare the cycles of gonad activity with the periods of seasonal abundance in the different sampling areas. In Fig.16 data are presented to show that grunter are abundant in St. Lucia estuary and lake from August to about February/March. From the cycle of gonad activity (Fig.23) it is apparent that in the estuary some of these fish have partially spawned gonads and will return to sea, but that most specimens are in a spent condition. It is mainly these fish which move into the lake and which subsequently either return to sea or remain in the system with gonads that have reverted to inactivity.

In the Durban marine sample the species was most abundant from September to February which is during the spawning and post-spawning phases of the reproductive cycle. At other times of the year it still occurs in this area but is mainly in an inactive condition.

The role of the different areas in the reproductive cycle can be summarised as follows (see Fig.22): spawning occurs at sea in the shallow inshore zone (and possibly also in slightly deeper water where sampling of gonad development are virtually absent (N = 2). Spawning has not been recorded in the lake. The occurrence of some partially spawned (N = 16) and spent (N = 25) specimens from June to November indicates that there is a slight tendency for these stages to enter the system, but viewed against the total sample of 682 specimens it is clear that they constitute a minority of the population.

(iii) Other Natal estuaries

The pattern of gonad condition is essentially similar to that already described for St. Lucia estuary.

(iv) Marine inshore environment

The data presented in Fig.24 are based on catches taken in the Durban area and in northern Zululand. It is apparent that inactive fish occur throughout the year but there is little evidence of when gonad development takes place. A few active specimens (N = 13) were recorded from May to August (1972 and 1973) but the occurrence of ripe running specimens from May onwards indicates that the initial stages of development must start considerably earlier than this.

An interesting feature is the relatively high proportion of ripe running (9.7%) and partially spawned (24.7%) fish obtained from both Durban and northern Zululand. Inshore spawning thus occurs along a considerable stretch of coast. Spawning fish were obtained over an eight month period extending from May to December, but the smaller proportion of ripe running and partially spawned gonads in May, June and December seems to indicate that the main season is from July to November.

In addition to the above a sample of 85 specimens was obtained from the vicinity of Inhaca Island, Mozambique. The gonad stages of these fish are set out in Table 7. In April most gonads were inactive, but some were in active condition. This is earlier than this stage has been recorded in Natal but was predicted on the basis of the appearance of ripe running specimens in the Natal sample (see above). The July catch is very interesting for not only does it include pre-spawning gonad stages, but it is dominated by ripe running fish. Inhaca Island appears to be an important spawning area for R. sarba.

(v) Discussion

A very significant fact emerges when the season of inshore abundance (Fig.18) is compared with the cycle of gonad activity (Fig.24). From this it is clear that R. sarba is most abundant from May to November and that this period coincides with the spawning season. As pre-spawning fish with developing gonads are virtually absent from this zone there is evidence of an inshore movement in order to undertake this fundamental biological function.

It is apparent from Fig.24 that inactive specimens are present in all the sampling areas throughout the year and that the other gonad stages are more seasonal in their occurrence. Furthermore inactive fish constitute the bulk of the overall catch (Fig.22) and can therefore be considered quantitatively to be the most important component of the inshore and estuarine populations. It should perhaps be pointed out that the occurrence of inactive gonads throughout the year is likely to arise from the long breeding season (8 months) which enables early spawners to revert to inactivity before the end of the season, and conversely, for late spawners to be inactive at the start of the season.

In Section 6.3 mention was made of the fact that no marked seasonal trend in abundance of R. sarba had been detected in St. Lucia and little was known about its movements through the Narrows. Reproduction studies do, however, provide some indication of the period of migration into the system. These data (Fig.24) show that most post-spawning fish occur in the estuary from June until November and that this coincides with their appearance and duration of occurrence in the lake. Since spawning occurs at sea these specimens must move into the estuary and thence into the lake, where with time the gonads of those that remain revert to inactivity.

Certain aspects of the return migration to sea can also be inferred. The predominance of inactive fish in the estuary suggests that migrants will be mainly in this phase of the reproductive cycle, while their presence throughout the year and the lack of any marked seasonality might arise from the fact that the species has a long spawning season. Thus the occurrence of maturing gonads is also likely to be spread over a long period, and as this phase takes place at sea, the movement of inactives through the Narrows as a prelude to gonad development would tend to be regulated accordingly. This suggests that the inactives in the Narrows constitute a dynamic migrating population rather than a static resident one.

Argyrosomus hololepidotus

(i) *Estuarine environment*

Samples from the St. Lucia system and from other estuaries (Fig.25) indicate that inactive fish are present throughout the year and it is clear that this gonad stage predominates in all these areas (Fig.22). Spent fish are the only others that have been recorded and although present in small numbers, occur seasonally during the period June to November. This was detected in each of the three years 1968 - 1970.

(ii) *Marine environment*

Essentially the same pattern is apparent from the marine data. Inactives occur throughout the year (Fig.25) and dominate the catch (Fig.22), while spents were recorded in June, July, September and October.

In addition two specimens with partially spawned gonads were obtained during July but there can be no certainty as to whether further spawning would have occurred or whether these gonads were regressing to the spent condition.

(iii) Discussion

The complete lack of evidence of gonad development in research samples, together with the fact that limited numbers of this species are encountered locally in deep water by commercial line boats, makes the occurrence of extensive spawning in Natal seem unlikely. However, it is possible that some does take place in deep water and that this accounts for the movement of juveniles (from 5cm in length) into St. Lucia during the summer months (see Section 8.3.2).

In a large species such as the kob longshore migrations can be expected and it is therefore considered likely that the inactive specimens in the Natal region move elsewhere on the South African coast to spawn. The appearance in Natal of spent fish at the time of the year when the species' abundance increases as a result of movement up the coast (see Section 6.3), provides circumstantial evidence that spawning occurs in the cooler waters of the Cape. The only published information to this effect (Day, 1967) concerns a single ripe female of 88.5cm trawled off Cape Infanta in 80m.

The appearance of spent fish in St. Lucia estuary and lake indicates that some of these specimens move into estuarine systems. However the presence of inactive specimens in estuaries and at sea throughout the year is puzzling. Whether it is due to specimens missing a spawning or whether there is an extended breeding season and part of the population is consequently always inactive, has yet to be established.

<u>Liza macrolepis</u> (Fig.26)

(i) <u>St. Lucia estuary</u>

Very few fish with gonads in active and active-ripe condition were recorded; but specimens with ripe gonads were obtained from March to November. Spents have been recorded during most months of the year but those from January to April are in an advanced stage of regression. It is interesting that eight females with translucent ova were netted about 4km within the estuary during August (1970), September (1969) and November (1969), thus indicating that they were on the point of spawning (classed under ripe running in Fig.26). However no spawning has actually been recorded in the estuary and it is unlikely that it takes place under estuarine conditions because gonad resorption was recorded when the mouth was sanded up from early June to the end of August 1970 (represented by hatching in Fig.26, more details under <u>M. cephalus</u>).

Additional information on spawning was obtained in 1971 when extensive shoals of mullet were observed in the St. Lucia mouth at night during June, July and August. Specimens captured in throw nets included true ripe running <u>L. macrolepis</u> and spawning can therefore be considered to take place in the vicinity of the entrance of this estuarine system.

Large numbers of spent fish occur in the estuary.

(ii) <u>St. Lucia lake</u>

Very few specimens with gonads in active and active-ripe condition were recorded but since most of the specimens were obtained from the south lake it is possible that these gonad stages occur elsewhere in the system. Fish with ripe gonads were obtained throughout the year but were present in greatest numbers from about May to August. Spent fish are also present throughout the year. No ripe running fish have been sampled in this area.

(iii) Other Natal estuaries

A similar pattern of gonad activity to that in St. Lucia estuary has been recorded. A female in true ripe running condition was netted in the tidal basin about 100m inside the mouth at Kosi Bay in August, and a specimen with translucent but not running eggs was obtained in Richards Bay in October.

(iv) Discussion

On the basis of the data presented above it is apparent that most spawning takes place from May to November. The statement by Day and Morgans (1956) that this occurs in winter should therefore be extended to include spring. There is evidence that spawning takes place in the vicinity of the estuary mouths of Kosi Bay, St. Lucia and Richards Bay and there is no reason to doubt that it also occurs elsewhere in Natal under similar conditions.

In estuarine areas ripe and spent fish constitute the bulk of the adult population (Fig.27). In St. Lucia lake ripe specimens slightly outnumbered post spawners and as there is no evidence of spawning in this area it seems clear that ripe mullet migrate seawards to spawn. This tends to confirm the proposal made in Section 6.3 that a seaward migration from St. Lucia was responsible for the seasonal increase in abundance in the south lake and estuary. However the occurrence of spent fish in the south lake indicates that there is also a return migration of post-spawners.

Liza dumerili (Fig.28)

(i) St. Lucia estuary

The species occurs in this area seasonally from July to November (Section 6.3) and during this period the gonads are mainly in ripe and spent condition.

Seven specimens with true ripe running gonads were netted in the estuary about 4km from the mouth (July and August 1969) but extensive spawning does not appear to take place. However during June, July and August 1971 large shoals of mullet were observed in the mouth and when these were sampled by means of throw nets were found to include L. dumerili in spawning condition (not included in Fig.28).

(ii) St. Lucia lake

The relatively few specimens examined (N = 66) had gonads in ripe, spent and inactive condition; no spawning has been recorded in the lake.

(iii) Other Natal estuaries

The species was sampled throughout the year in these estuaries, the gonads being mainly in ripe, spent and inactive condition. Ripe specimens were recorded from April to December. A single specimen in true ripe running condition was netted in Richards Bay (June, 1970).

(iv) Discussion

It is apparent from Fig. 27 that ripe, spent and inactive fish constituted the bulk of the estuarine catch. No ripe running specimens were recorded in St. Lucia lake and as only eight were sampled in estuarine areas and these were in close proximity to the sea, it seems that spawning does not generally occur in the estuarine environment. However the presence of large numbers of specimens with ripe running gonads in the St. Lucia mouth indicates that spawning is also likely to take place elsewhere under similar circumstances.

Ripe running fish have been obtained in June, July and August and a few ripe specimens are present as late as December. The statement by Day and Morgans (1956) that spawning occurs between winter and spring is thus confirmed by the present study but should be extended to include early summer.

7.2.2.2 Other species

Acanthopagrus berda (Fig.29)

(i) Natal estuaries

The species is mainly spent or inactive when it occurs in the estuarine environment. However the occurrence of ripe gonads and the proportion of spent fish provide evidence that the spawning season is likely to fall within the period May to August, spawning possibly being most intense in May and June. During these two months three ripe running specimens were gill netted 300m inside the St. Lucia estuary mouth over a high tide cycle, and another three were obtained from anglers fishing in the mouth itself. Spawning close inshore in the vicinity of estuary mouths can thus be considered to occur in *A. berda*, but the absence of ripe running specimens in catches taken at the standard netting localities in St. Lucia estuary (± 4km from the mouth), in St. Lucia lake and in Richards Bay indicate that this does not take place under true estuarine conditions.

(ii) Marine environment

Although very few specimens have been examined, the occurrence of ripe and spent gonads in May suggests that this month falls within the spawning season and hence serves to confirm the evidence to this effect obtained from estuarine sampling.

Elops machnata (Fig.29)

(i) Natal estuaries

Very little is known about the reproductive biology of this species. It is inactive throughout the year and with the exception of a single active specimen, this is the only gonad stage that has been recorded.

(ii) Marine environment

Only 12 specimens have been examined and all had inactive gonads.

(iii) Discussion

Nothing is known about the gonad development, spawning or post-spawning phases of the life cycle of this species. None of these occur in Natal estuaries and marine sampling did not provide an indication of whether they occur in Natal waters.

Johnius belengerii (Fig.30)

Estuarine and marine environments

A large proportion of the estuarine catch is spent or inactive. However ripe specimens occur from September to February and six females with translucent but not running ova have been recorded in the months September, October, December, January and February. In addition, one out of a total of four specimens obtained at sea from the Tugela Banks in September 1971 was a female in the same condition as those above. Spawning can therefore be concluded to take place during the six month period September to February.

The six specimens with translucent ova were recorded from Richards Bay (1), St. Lucia north Narrows (3) and St. Lucia south lake (2), but as they were not actually in running condition and made up a small proportion of the total estuarine catch (N = 545) it seems unlikely that spawning is an estuarine activity. Some fish might shed their ova under estuarine conditions but since this species is abundant in shallow water on the Tugela Banks and off the St. Lucia mouth (Table 3), it seems probable that most move out of estuaries before this occurs.

Leiognathus equulus (Fig.30)

(i) Natal estuaries

Gonads are mainly spent or inactive in the estuarine environment but fair numbers of active, active-ripe and ripe gonads have also been recorded. No ripe running fish have been sampled but the occurrence of ripe and spent fish suggests that spawning extends from September to April, possibly being more intense from about October to March.

(ii) Marine environment

Very few specimens have been examined. However the data reveal that some fish have active gonads in June and the presence of partially spawned fish in December tends to confirm that this month falls within the spawning season.

Liza tricuspidens (Fig.31)

(i) Natal estuaries

Only fish with spent and inactive gonads have been recorded.

(ii) Marine environment

Ripe and partially spawned gonads were recorded in September and a ripe running fish was obtained from the surf zone in the Durban area during November. There is thus evidence of spawning from September to November, but the occurrence of spent fish in July, August and December suggests that it actually extends over a considerably longer period.

Otolithes ruber (Fig.31)

(i) Natal estuaries

Most fish are spent and inactive in this environment. However the occurrence of ripe specimens from September to November and spents from October to December suggests that spawning occurs in spring and early summer.

(ii) Marine environment

This pattern tends to be confirmed by the marine sample but the presence of partially spawned fish in January and February, and of three ripe running fish in February (Durban area), indicates that spawning also extends throughout the summer.

Pomadasys hasta (Fig.32)

(i) Natal estuaries

This species is mainly inactive in the estuarine environment.

(ii) Marine environment

A small sample (N = 14) obtained from 30 - 40m on the Tugela Banks in June 1972 included three specimens with ripe running and nine with partially spawned gonads. Spawning obviously takes place during winter but in the absence of additional data its duration remains unknown.

Rhabdosargus holubi (Fig.32)

(i) Natal estuaries

The species is mainly inactive or spent when it occurs in the estuarine environment. However some indication of the spawning season is provided by the fact that spents have only been recorded from May to August; while the inclusion of two ripe running females in a sample from Durban Bay in August 1970 provides evidence that this month falls within the spawning season.

Spawning is, however, unlikely to occur to any great extent in Durban Bay as adults are not abundant under present-day conditions (only 37 adults were netted) and because no ripe fish were obtained. This is in accordance with the findings of Day and Morgans (1956) who studied the fauna before gross environmental degradation had occurred and who did not record any ripe or ripe running R. holubi. On the basis of this evidence and the fact that the Bay has sea salinities and a deeply dredged mouth (a full description is given under Section 3.3.3), it seems reasonable to consider the two ripe running specimens to be part of an inshore spawning population.

(ii) Marine environment

The occurrence in the Durban area of specimens with ripe running and partially spawned gonads confirms the conclusion based on estuarine sampling that the spawning season falls within the period May to August.

Hilsa kelee (Fig.33)

Natal estuaries

The species is mainly spent or inactive in estuarine areas. Nevertheless some ripe specimens have been recorded between September and February and it is probable that this period approximates the spawning season. The occurrence of spawning in December is indicated by the two ripe running fish recorded in Durban Bay, but since the salinity of this area approximates that of the sea this record is considered to be indicative of local spawning in shallow inshore waters.

Valamugil buchanani (Fig.33)

Natal estuaries

The gonads are mainly inactive and spent when this species occurs in estuaries. However from the pre-spawning gonad stages which do occur it appears that spawning takes place in spring and is likely to extend into summer. There is no evidence of spawning in estuaries.

Valamugil cunnesius (Fig.33)

Natal estuaries

Specimens in ripe condition have been recorded during most months of the year and it thus appears that there is an extended spawning season. Two ripe running females were netted 4km inside St. Lucia estuary during March and May but as this gonad stage was not recorded in the other sampling areas spawning does not seem to be an estuarine function. However, viewed together with the large proportion of ripe and spent specimens, it seems reasonable to interpret the presence of these individuals as being indicative of spawning inshore in in the vicinity of estuary mouths.

Solea bleekeri (Fig.34)

Natal estuaries

Gonad maturation has been recorded during March, April, May and June; and ripe running specimens have been obtained in June, July and August. There is therefore evidence that spawning takes place under estuarine conditions and it is interesting that a ripe running specimen was obtained at a salinity level of 47 $^{0}/_{00}$ in St. Lucia lake.

Thryssa vitrirostris (Fig.34)

(i) St. Lucia Estuary, Richards Bay and Durban Bay

Ripe specimens have been recorded from August to January and ripe running fish during September, October and November. The latter were only obtained from St. Lucia estuary.

(ii) St. Lucia lake

Large numbers of ripe running specimens have been recorded in September, October, November and December, and some have been obtained as late as March. The salinities at which these specimens were netted ranged from 35 - 45 $^{0}/_{00}$.

These data reveal that T. vitrirostris spawns in St. Lucia; spring and early summer apparently being the periods of major reproductive activity. However plankton net catches (Section 7.2.2.4) cast doubt on whether viable young were produced.

7.2.2.3 Miscellaneous species

The data obtained from species sampled in limited numbers have been presented in Tables 8 and 9, which include comments on seasons and areas of spawning. It is apparent from Table 8 that species which are relatively uncommon in Natal estuaries tend to occur in this environment during their periods of least reproductive activity (when gonads are in spent and inactive condition).

Ambassis natalensis, Gilchristella aestureus and Hyphorhamphus knysnaensis have been found to spawn in Natal estuaries (details in Table 9). All three are small species which are very abundant in estuaries and do not seem to depend on a marine phase in their life cycles. They are apparently somewhat similar to Gobius giuris which according to Smith (1949) and Crass (1964) has colonised estuarine and freshwaters where it lives and breeds without having to return to sea. In view of the fact that the present programme did not place emphasis on the study of small fishes of little direct significance to man, it is very likely that more species spawn in estuaries than the above data indicate.

7.2.2.4 Larval fishes caught in the plankton

Catches have been summarised as follows:

(i) St. Lucia south lake

Ambassis spp.: The characteristic pre-opercular spines as well as vertebral counts enabled larvae to be recognised down to 5mm. Catches included many larvae as small as 3mm (which still had remnants of their yolk sacs) and which appeared to be Ambassids.

Gilchristella aestuareus: Specimens could be identified down to about 15mm. Some as small as 10mm resembled this species.

Family Gobiidae: Specimens down to about 10mm appeared to belong to this family.

Family Hemirhamphidae: Specimens of about 14mm could be identified by the slight bulge at the tip of the lower jaw. Below this length identification became dubious.

Thryssa vitrirostris: The smallest specimen recorded was 26mm in length despite the fact that the elongated serrated maxilla makes it possible to identify this species down to about 15mm.

(ii) St. Lucia estuary

Ambassis spp.: Larvae identified down to 8mm.

Gilchristella aestuareus: Specimens down to about 15mm.
Family Gobiidae: Specimens down to about 10mm.
Family Hemirhamphidae: A few specimens down to 42mm.

Leiognathus equulus: Specimens down to 16mm.

Liza macrolepis: A few specimens down to 14mm.

Mugil cephalus: A few specimens down to 15mm.

Rhabdosargus sarba: Two specimens of 11 and 12mm.

Therapon jarbua: Numerous specimens down to 12mm.

Thryssa vitrirostris: Numerous specimens between 15-58mm.

Unidentifiable: Large numbers of larvae with yolk sacs ($\pm$ 3mm), possibly mullet spp.

Comparison of the data from these two localities reveals that a greater variety of species was recorded in St. Lucia estuary, where larvae of *L. equulus*, *L. macrolepis*, *M. cephalus*, *R. sarba* and *T. jarbua* were included in the catch. Their absence from the lake suggests that spawning does not occur in this environment and is in keeping with the evidence obtained from the study of the gonads of adults.

It seems probable that their presence in the estuary arises from larvae being washed in from the sea, rather than from spawning under estuarine conditions.

The other species were recorded from both localities, catches in the lake being more indicative of whether spawning occurs in estuaries. The presence of large numbers of very small *Ambassis* larvae indicates that spawning takes place in the lake. This supports the evidence presented earlier (Table 9) that *A. natalensis* spawns under estuarine conditions and it is possible that other species such as *A. gymnocephalus* do so as well.

Larvae of G. aestuareus were extremely abundant in the lake during the sampling period and were recorded in salinities up to 47 $^0/_{oo}$, suggesting that spawning occurred under hypersaline conditions. Allanson et al (1966) report the presence of this species in the landlocked Lake Sibayi where it spawns in freshwater. It is therefore apparent that G. aestuareus is an extremely versatile species able to spawn under varying environmental conditions.

The occurrence of larvae of the families Gobiidae and Hemirhamphidae in the lake constitutes evidence that spawning takes place in the system. Although the gonad cycle of adult gobies has not been studied, the presence of ripe running specimens of Hyporhamphus knysnaensis in estuaries has already been reported (Table 9).

Somewhat conflicting evidence has been obtained concerning the spawning habits of T. vitrirostris. Ripe running adults have been recorded in the lake in large numbers (Fig.34) but the smallest specimen netted in the plankton was 26mm in length. The possibility that smaller specimens were present in the lake and were not sampled cannot be entirely discounted, but the fact that larvae as small as 15mm were obtained in the estuary suggests that they would have been netted in the lake had they occurred there. Planktonic evidence thus tends to indicate that spawning occurs at sea, not in estuaries, and that the ripe running adults in the lake failed to produce viable young. This might have been a consequence of the hypersaline conditions prevalent at that time.

Further research is obviously needed in order to clarify the spawning habits of this species.

7.3 Length at sexual maturity

7.3.1 Methods

Fish with gonads that range in condition from active to spent are easily identified as being sexually mature, but it can be difficult to distinguish macroscopically between the inactive gonads of mature fish and the undeveloped gonads of immature specimens. This problem is generally most acute in the adolescent length range.

In this study no attempt has been made to distinguish between inactive and immature gonads; the estimates of length at maturity being based entirely upon fish with gonads ranging from active to spent condition.

7.3.2 Results

For the main species the data have been presented graphically (Fig.35) by expressing the number of mature fish in each length class as a percentage of the total number in that class (including inactives and immatures). The adolescent length range is indicated by the increasing proportion of matures and corresponding decrease of immature/inactives. When the proportion of these two groups reaches approximate equilibrium the population can be considered to be completely mature. The length at which this is estimated to occur has been arrowed. Sexes have been lumped when differences in length at maturity were not detected.

In the other species the actual number of mature (active to spent) and immature/inactive fish has been recorded (Table 10). Asterisks indicate the length classes from which all specimens were included in the study of the cycle of gonad activity (Section 7.2).

Information on the lengths of attainment of sexual maturity is useful from a practical management point of view as a commonly applied conservation measure is to legislate against the capture of sexually immature fish. However this will not be elaborated here as the need to restrict the length of the thesis precludes consideration of detailed management proposals for individual species. Suffice to say that recommendations based on these data have been presented to the Natal Parks Board and in the case of P. commersonni and R. sarba have already been incorporated into the Natal Provincial Fisheries Ordinance.

7.4 Discussion

The object of this discussion is to draw attention to the main characteristics of reproduction in the estuarine fish fauna. The results for individual species have already been discussed under the separate species headings and will not be repeated here.

A summary of the data obtained on areas of spawning is presented in Table 11. An obvious fact to emerge is that most species spawn at sea. In seeking reasons for this it is important to recognise that the species which occur in Natal estuaries are actually those members of the shallow marine fauna which are able to adapt to the variable conditions found in the estuarine environment. Many marine species do not enter estuaries and it is clear that the conditions of salinity, turbidity and temperature (see Section 2.3) make this both a specialised and harsh environment. This is particularly true during spring and summer when the steep topography and heavy rainfall typical of the eastern part of South Africa cause strong river outflow, high turbidities and widely fluctuating salinities.

Against this background must be borne in mind the fact that the spawning seasons of a number of dominant estuarine species (such as P. commersonni, R. sarba and L. macrolepis) extend into this period of the year, and that as far as is known these species shed their gonadal products freely into the water and do not exercise any parental care of the young (in contrast to many freshwater fishes living in East Coast rivers). As Breder and Rosen (1966) point out, a successful reproductive mechanism is basic to the survival of the species and it is therefore necessary for this mechanism to develop so as to reduce to a minimum any chances of failure. Since conditions in East Coast estuaries can hardly be considered favourable for the survival of egg and larval stages, and since most species are active swimmers, it is not surprising that their reproductive mechanism involves migration out of estuaries to spawn in the relatively stable marine environment.

On the East Coast, with its high frequency of small estuaries and low incidence of big ones, it is possible that estuarine spawning would have the added disadvantage that large species which are present in relatively small numbers (e.g. P. commersonni) would have difficulty in forming the large shoals generally associated with group spawning in teleosts. Presumably the smaller the estuary the greater the problem. A reproductive mechanism which involves migration to sea and the congregation of fish in specific spawning grounds would appear to have advantages in overcoming this problem. Greater dispersion of offspring would also seem more likely to occur as a result of marine spawning.

Insight into the location of the marine spawning grounds of certain estuarine species has been obtained (Table 11). Three species (A. berda, L. dumerili and L. macrolepis) have been found to spawn in the immediate vicinity of estuary mouths and it seems probable that they also spawn in the inshore environment. In addition, evidence of inshore spawning has been obtained for a further nine species. Of these, the most comprehensive data are available for P. commersonni and R. sarba. In both species specimens with developing gonads are rare in the estuarine and inshore environments and it is apparent that this phase of the reproductive cycle occurs elsewhere, probably at sea in slightly deeper water. In marked contrast to this is the fact that ripe running and partially spawned specimens have been recorded in relatively large numbers inshore and that these gonad stages occur at the time of the year when both species increase in abundance. This suggests that P. commersonni and R. sarba move inshore to spawn.

M. cephalus is another species which increases dramatically in abundance in inshore waters and although actual ripe running specimens have not been obtained, the weight of circumstantial evidence indicates that spawning occurs in this environment (see results for details). Available evidence indicates that other species such as V. cunnesius and R. holubi also spawn inshore.

It is significant that the dominant estuarine species for which data are available all spawn in the vicinity of estuary mouths or in the inshore marine environment. If one takes into account the fact that the juveniles of these species are very abundant in estuaries, and that there are distinct problems associated with estuarine spawning, one is led to the conclusion that the reproductive mechanism has evolved so as to take advantage of the stability of the marine environment and yet to produce offspring where they can migrate into estuaries at an early stage in their lives. This mechanism would appear to have definite survival value on the East Coast, which is characterised by its narrow continental shelf and the strong Agulhas Current that flows south westwards towards the South Coast region where the temperate inshore and estuarine conditions are unfavourable for subtropical species.

To complete this review of the data obtained on areas of spawning attention must be drawn to the relatively few species which spawn in estuaries (see Table 11). These have rather specialised life histories and were not studied in detail in the present programme. There is consequently considerable scope for additional research on this group.

A. natalensis, G. aestuareus and H. knysnaensis are small species that are extremely abundant in Natal estuaries where they have been recorded in ripe running condition and their larvae have been netted in the plankton. The ability of these and related species to spawn in conditions of lowered salinity and even in freshwater has been reported in the literature. Breder and Rosen (1966) state that a species of Ambassis (under the name Chanda lala (Hamilton-Buchanan)) is fully adapted to life and reproduction in freshwater. Allanson et al (1966) record that G. aestuareus occurs in the landlocked freshwater Lake Sibayi (northern Zululand). Smith (1933) reports the occurrence of ripe H. knysnaensis in tidal rivers and in this context describes their eggs as 'demersal, 1.6mm in diameter, almost transparent and densely covered with glutinous hair-like filaments considerably longer than the diameter of the egg'. According to Breder and Rosen (1966) these serve to attach the eggs to weeds and other objects.

It would be interesting to investigate the factors responsible for these estuarine/freshwater spawning habits and the specialisations in their reproductive biology which enable these species to depart from the general trend of marine spawning typical of the estuarine fish fauna. Factors which may play a part are their small size, abundance in estuaries where spawning shoals can easily be formed, and less physical ability to undertake migrations to and from the sea than large species.

Larvae of the family Gobiidae were netted in the plankton in St. Lucia lake and it seems probable that one or more species breed under estuarine conditions. Specialisations in Gobiid breeding biology reported by Breder and Rosen (1966) include: adhesive eggs which are laid in excavations in the substrate, under stones, amongst algal filaments, and even in the case of one species in the burrows of the mud prawn Upogebia. Parental care is common, the male usually guarding the nest. Reference is also made to the fact that these mechanisms allow eggs to be laid in rapidly flowing streams. These specialisations would obviously equip members of this Family to overcome many of the problems associated with estuarine spawning and could provide a fascinating field of study.

A summary of the months of spawning is provided in Fig.36. It is apparent that 13 species complete their spawning during late autumn, winter and spring (May to November) and it is interesting that this group includes the dominant estuarine species of the Natal region. An additional eight species complete most of their spawning during spring and summer (September to February) and, with the exception of H. knysnaensis, are much more abundant inshore and in shallow water on the continental shelf than in estuaries (details in Table 3). The last three species in Fig.36 are not abundant in Natal estuaries and evidence of spawning has only been obtained during summer. More comprehensive sampling would probably indicate that spawning extends over a somewhat longer period.

It seems highly probable that the seasonality of spawning of the dominant estuarine species is biologically significant. Data obtained from the study of recruitment of juveniles into estuaries suggests that this is an adaptation which enables juveniles to migrate into estuaries before the summer rainfall season of strong river outflow (see discussion Section 8). Further consideration of this interesting possibility is included in the general discussion (Section 9) where evidence from the study of reproduction and recruitment is collated.

It is apparent from Fig.36 that most species have an extended spawning season lasting from four to six months and that some species spawn during as many as eight months of the year. It is difficult to assess whether this is a significant feature of the breeding cycle of estuarine species because comparison with typically marine fish is hampered by the fact that data are only available for two species in Natal waters. Ahrens (1964) showed that the

'Seventy Four' (Polysteganus undulosus) spawns during the three months September to November; while van der Elst (1974) has found that the elf (Pomatomus saltatrix) spawns during the four months October to January. As both these seasons start later and are of shorter duration than those of the dominant estuarine species, there is some evidence that there are differences between the spawning habits of these two groups of fishes.

A possible reason for the extended spawning season in estuarine species is that it prolongs the period during which fry occur in the inshore environment. On the East and South coasts of South Africa, which have a high frequency of blind estuaries, this would increase the probability of each estuary opening during the recruitment phase of the life cycle. It would also increase the chances of successful estuarine recruitment in the event of floods occurring during the period of peak immigration of fry (the relationship between seasons of recruitment and river outflow is discussed in Section 8). Thus an extended spawning season which gives rise to a prolonged recruitment period would appear to have a 'buffering' action against failure of recruitment as a result of adverse climatic conditions.

7.5 Summary and Conclusions

1. Most species spawn at sea despite the fact that they are adapted to the variable environmental conditions typical of estuaries. It is suggested that this is because the relatively stable marine environment is more suitable for the survival of egg and larval stages.

2. Evidence is presented to show that the spawning grounds of the dominant estuarine species are located inshore and in the vicinity of estuary mouths.

3. Spawning is likely to occur in this environment so as

to increase the chances of juveniles migrating into East Coast estuaries, instead of becoming transported to the less favourable South Coast region by the Agulhas Current.

4. Certain small species do spawn in estuaries and seem to have overcome the problems associated with spawning in this environment by developing specialised reproductive mechanisms.

5. The spawning season of the dominant estuarine species is during late autumn, winter and spring (May to November) and it is suggested that this enables juveniles to migrate into estuaries before the summer rainfall season of strong river outflow.

6. The dominant estuarine species have extended spawning seasons lasting 4 - 8 months. This prolongs the period of juvenile recruitment and appears to have a 'buffering' action against failure of recruitment as a result of droughts or unseasonal floods.

7. Emigration of adult fish from estuaries is usually related to the need to spawn at sea. Many species migrate into estuaries during the post-spawning and inactive phases of their reproductive cycles.

8. RECRUITMENT OF JUVENILES INTO ESTUARIES AND ASPECTS OF THEIR BIOLOGY IN THIS ENVIRONMENT

8.1 Introduction

The role of estuaries in providing nursery areas for juvenile fishes has been mentioned by workers in various parts of the world. Particular attention has consequently been paid to investigating whether this function is of importance in the biology of the estuarine fish fauna of the East Coast of South Africa. To do this adequately it was necessary to collect data on as many species as possible and to supplement the regular sampling programme in Natal with a survey of the occurrence of juveniles in Transkei and South Coast estuaries.

8.2 Methods

Details of the routine sampling programme have already been given in Section 3.4 and will not be repeated here.

The main problem encountered in this phase of research was the identification of juvenile fish when they first migrate into estuaries. This was most acute in the Mugilidae (mullet), a group in which much of the taxonomic literature relies upon criteria which are not definitive when applied to juveniles. These problems were overcome by following different morphological characteristics down the size range of reference collections which consisted of fry netted in the wild, grown in the laboratory and killed at regular intervals. As a result it was found possible to identify the smallest specimens that occur in estuaries (10 - 20mm total length) by utilising a combination of lateral line scale counts and features of dentition (van der Elst and Wallace, in press). This laboratory procedure was also applied to other species for which identification problems were encountered.

Owing to the selectivity of the netting gear used to sample juveniles, catches generally consisted of specimens less than 20cm in length. This has consequently been used as the upper limit of size included in the analysis and presentation of the results. The small number of larger specimens that were netted have been incorporated into sections dealing with 'adult' phases of estuarine fish biology.

Catches have been grouped into 1cm length classes and in the case of species that were sampled in large numbers have been presented as monthly percentage frequency distributions. In other species the actual number of fish have been tabulated.

These data indicate the months of onset and duration of recruitment into estuaries, as well as the lower range of size over which these migrations take place. Insight into the immigration of larger size classes cannot be obtained from these data as there is no way of determining whether the specimens comprise new arrivals or whether they have spent some time in the estuarine environment.

Estimates of juvenile growth rate have been made for five species. However it has not always been possible to use the Petersen method of modal progression and monthly increases in the mean length of catches have had to be utilised. Further details are given under the results for the species concerned.

In order to gain insight into the geographic extent of utilisation of estuaries by juveniles of species that occur in Natal, sampling was undertaken in selected estuaries along the East, South and West coasts of South Africa during November 1973. This month was chosen because studies of reproduction of adults and recruitment of juveniles had indicated that most recruitment was likely to have taken place by the end of spring. Due to this careful timing of the survey it was possible to obtain valuable results (Tables 13 and 14) despite the fact that the large distances prevented more than one expedition from being conducted. Catches reported by Talbot (1955) for the Klein river have been incorporated into the results.

8.3 Results

8.3.1 Species composition of juvenile fauna

The 54 species that have been recorded in Natal estuaries during the juvenile phase of their lives are listed in Table 12, which also includes an estimate of their relative abundance and comments on their 'usefulness to man'.

It is apparent that juveniles of 20 angling species, and of 10 non-angling species valuable as human food, occur in Natal estuaries. The remainder are generally small species that provide food for predatory fish which enter estuaries during their adult phase of life and are exploited as a sport angling resource.

Juveniles of 29 species are considered to be abundant, very common or common. Particular attention has been paid to the species in this group which are of major importance in Natal.

8.3.2 Recruitment, growth and distribution

Mugil cephalus

Length at recruitment

Despite extensive sampling with plankton, box and scoop nets, specimens less than 11mm in length have not been recorded in Natal estuaries and it is apparent that the earliest stages in the life cycle occur at sea. Sampling during the years 1969 to 1971 has revealed that the inward migration starts when fry are in the 1-2cm length class and seems to be most intense within the 1-4cm length range (Figs.37 and 38). Recruitment continues amongst larger specimens but netting in the St. Lucia estuary, where the shoals tend to be moving from the sea towards the lake, suggests that this is quantitatively less significant than for the smaller length classes.

Month of onset and duration of recruitment

In 1971 (Fig.38) 1-3cm fry were recorded from June to October. This is considered to be the period of major estuarine recruitment, although there is evidence that it continues with lower intensity during November and December (see 1969/70 data, Fig.37). The absence of fry from the June 1969/70 catch has probably resulted from the relatively low sampling effort with the drag and scoop nets at that stage of the programme.

Rate of growth of juvenile recruits

Monthly catches (Figs.37 and 38) do not form a modal series suitable for making detailed estimates of juvenile growth rate. This is largely due to the combined effects of gear selectivity and the prolonged recruitment period. However a growth effect is apparent from the 1971/72 data which show that by March 1972 most of the specimens sampled were between 120 and 160mm in length. As the smaller specimens in this range are likely to have entered estuaries towards the end of the recruitment period, it seems reasonable to relate the upper end of this range to the early recruitment of June/ July. Specimens approximately 150mm in length would thus have been in the estuaries for 8 - 9 months and have grown at about 17 - 19mm per month. This gives an estimate of 200 - 230mm total length at one year and is similar to estimates obtained from scale annuli in eastern and western Australia and in western Florida (quoted by Thomson, 1963), which range from 140 - 179mm standard length at one year (equivalent to 185 - 230mm total length).

Occurrence in South African estuaries

It is apparent from Table 13 that juveniles are widely distributed in estuaries on the East and South coasts of South Africa. As this applies to the smallest length class (0 - 3cm), which has been recorded from the Kosi Lakes to the Breede River (localities shown in Fig.2), it seems probable that spawning is also widespread.

Pomadasys commersonni

Length at recruitment

Grunter fry less than 2cm in length have not been recorded in Natal estuaries despite sampling with plankton and box nets in the deeper exposed waters and with scoop nets in the marginal shallows (Fig.40). It is thus concluded that these young stages occur at sea and that migration into estuaries first takes place when fry are between 2 - 3cm in length. However neither this nor the 3 - 4cm length class were well represented in estuarine samples and it appears that most estuarine recruitment occurs when fry are between 4cm and about 7cm in length (Figs. 39 and 40). Whether recruitment of larger specimens also occurs is unclear due to the difficulty in distinguishing between new recruits and specimens which have been in the estuarine environment for some time.

Month of onset and duration of recruitment

The data obtained in 1971/72 (Fig.40) indicate that recruitment of specimens less than 5cm in length took place from September to December, and that relatively large numbers of 4 - 5cm fry were present as late as March.

The 1969/70 data (Fig.39) differ considerably from those above. Specimens of less than 5cm first appeared in July and disappeared from catches after December. These differences appear to arise from true variation in recruitment periods (sampling effort was high throughout 1971), but the factors responsible are unknown. Both sets of data reveal that recruitment occurs over a prolonged period of 6 - 7 months.

Rate of growth of juvenile recruits

In interpreting the results set out in Figs.39 and 40 it is essential to bear in mind the selection characteristics of the different nets used in the sampling programme. It can be seen from Fig.41 that the drag and seine nets have similar characteristics but that the shrimp trawl is less efficient in capturing the smaller length classes. Consequently any catch in which the shrimp trawl makes a big contribution is likely to have its mode biased to the right, and conversely, when the seine and/or drag net dominate the catch the mode will tend to move to the left. Use of the combined data to estimate juvenile growth rate is thus inadvisable.

A more accurate method is to estimate growth from the various nets during the months that it takes juveniles to grow through their different ranges of selectivity. As these ranges are rather narrow the estimates cover short periods, and the mean lengths of successive catches give a more accurate indication of growth than monthly modes which provide estimates in increments equivalent to the length class interval. Furthermore a mean can be calculated for a fairly small catch whereas a large number of individuals have to be sampled in order to obtain a well defined modal group

Catches suitable for growth determinations were obtained from the drag net and the shrimp trawl and covered a total length range of approximately 6 - 14cm.

In Fig.42 the mean lengths of monthly catches have been plotted and regression lines fitted by the least squares method. In the case of the drag net weighted means were used because the October sample was substantially smaller (N = 24) than samples for other months.

The similarity of the slopes of the different regressions suggests that the drag net and shrimp trawl catches are giving complementary estimates of juvenile growth rate. This is clear from Table 15 in which the slopes (or daily growth increments) are converted to monthly growth increments. These vary between 12.0-14.7cm. per month.

If 50mm is taken to represent the length at recruitment, and growth occurs at the estimated rate, juveniles will attain lengths of approximately 195 - 225mm during their first year in Natal estuaries. However this is possibly a slight overestimate since the monthly increments were calculated from catches taken from September to April and some reduction in growth rate might take place during winter.

Occurrence in South African estuaries

Juveniles of less than 3cm are uncommon in Natal estuaries (see above) and were not encountered elsewhere (Table 13). Specimens of 3 - 6cm were only recorded as far south as the Ntafufu river in the Transkei and larger specimens of 6 - 12cm as far as the Keiskamma and Kleinemond estuaries of the Eastern Cape. From this it appears that larger juveniles extend further to the south west, and that utilization of the estuarine environment is restricted to the warmer parts of the East Coast of South Africa. Spawning of adults also seems likely to be confined to this area.

Genus: Rhabdosargus

During the period of preliminary sampling (1969 and 1970) difficulty was experienced in identifying juveniles as they could not be distinguished by the criteria applied to adults or by features such as shape and colour. As the specimens sampled in estuaries resembled *R. sarba*, which was known to be very abundant in Natal, they were thought to belong to this species. That this was a mistake became apparent in 1971 when detailed study showed that juveniles of both *R. sarba* and *R. holubi* are abundant in Natal estuaries and that even the smallest specimens can be distinguished by the morphology of their incisor teeth. In *R. sarba* these are monocusped and peg-like, while those of *R. holubi* are distinctly tricuspid.

Due to this identification problem much of the 1969/70 data had to be discarded. Fortunately however, catches were preserved during the months when very small fry were sampled and it was subsequently possible to 'work back' through these collections to obtain evidence of when immigration took place.

Rhabdosargus sarba

Length at recruitment

No *R. sarba* larvae were caught with the plankton, box or scoop nets and it is considered that these stages occur at sea and not in Natal estuaries. The smallest specimens obtained were caught in the drag and juvenile seine nets and fell within the 2 - 3cm length class (Fig.43). However, smaller 'stumpnose' were observed escaping through the mesh and as some of these could have been *R. sarba*, it is possible that the earliest estuarine recruits are somewhat less than 2cm in length. However most recruitment appears to take place within the 2 - 5cm length range.

Month of onset and duration of recruitment

During 1971 estuarine recruitment started in August when fry of 2 - 3cm in length were first netted and this size class continued to be abundant during September (Fig.43). Growth of these recruits probably accounts for at least some of the 3-4cm specimens netted in October, but the general growth rate indicates that fry of this length caught during November and December 1971 and January 1972 are likely to be fresh recruits from the sea. This is also likely to apply to the 3 - 4cm specimens netted in January 1971. From these results it appears that estuarine recruitment of specimens less than 4cm in length takes place during the six month period August to January, but that it is most intense from August to November.

Little is known about the recruitment of specimens larger than 4cm owing to difficulties in distinguishing between individuals which have grown up in estuaries and those which are new recruits from the sea. However, it seems likely that they do migrate into estuaries.

Rate of growth of juvenile recruits

In this species interaction between the selectivity of different types of fishing gear has little influence on growth estimates because 87% of the total catch was obtained in the juvenile seine net. The modal series from August 1971 to January 1972 can therefore be used to estimate juvenile growth rate. During these five months the mode advances from 25mm (mid point of 2 - 3cm length class) to 95mm, giving a monthly growth increment of 14mm. The corresponding estimate calculated from the monthly mean length of the catch in the juvenile seine net (using the method described for P. commersonni) is 14.7mm per month (slope 0.482, N = 1054). A slower growth estimate of

10mm per month is obtained from the modal progression between January and May 1971 (75 - 115mm) but this is less likely to be representative of the population because the netting gear becomes less efficient as size increases and larger specimens are able to escape around the net.

It has not been possible to determine whether growth slows down during winter but the increase in length between August and September, when temperatures are still relatively low, suggests that there is not a marked reduction. If the recruits that enter estuaries in August at about 30mm grow at 14mm per month, a length of 190 - 200mm will be attained after a year.

Occurrence in South African estuaries

Specimens of less than 3cm have only been sampled as far south as Durban Bay and larger juveniles of 3 - 12cm as far as the Ntakatye River in the Transkei (Table 13). The juvenile phase of the life cycle of this species thus appears to be restricted to sub-tropical East Coast estuaries.

Rhabdosargus holubi

Length at recruitment

No larvae were sampled with the plankton, box or scoop nets and it seems probable that these stages of the life cycle occur at sea and not in Natal estuaries. The smallest specimens caught in the drag and juvenile seine nets were between 2 - 3cm, but smaller 'stumpnose' were observed escaping through the mesh. The fact that scoop net catches included specimens down to 13mm, suggests that many of the escapees were *R. holubi* and that estuarine recruitment starts at less than 2cm. Further evidence of this was provided by preserved collections taken in 1969 and 1970 which included many specimens of less than 2cm (Fig.44). Most recruitment appears to take place within the 1 - 5cm length classes (Figs.44 and 45).

Month of onset and duration of recruitment

It is apparent (Fig.45) that large numbers of fry of 2 - 4cm started migrating into estuaries in August and evidence presented above shows that smaller specimens were also involved. Catches in 1969 and 1970 confirm the 1971 data and in addition show that 1 - 2 cm specimens first enter estuaries in July. From this it is apparent that the main recruitment period for specimens in the 1 - 4cm length classes extends from July to November, with some immigration of 3 - 4cm juveniles continuing until as late as January. Slightly bigger specimens probably also enter estuaries.

Rate of growth of juvenile recruits

During the period August 1971 to January 1972 the monthly modal length class increases from 25mm to 65mm. This gives a monthly growth increment of 8mm. Over the period October 1971 to January 1972 good catches were made in the juvenile seine net in St. Lucia lake. The growth rate during this period, estimated from monthly means according to the method already described, is 8.5mm per month (slope 0.2815, N=1133). As there is an obvious increase in length between August and September (Fig.45) when temperatures are still relatively low, it seems unlikely that growth decreases much during winter in Zululand estuaries. It therefore seems reasonable to apply these growth rates throughout and to conclude that juveniles grow about 100mm in their first year (after entering estuaries at about 2 - 4cm). This is considerably more than in the warm temperate Kleinemond estuary where the growth increment in the first year was estimated to be 60mm and where a distinct reduction in growth was recorded during winter (Blaber, 1974).

Occurrence in South African estuaries

It is clear from Table 13 that juveniles (inclusive of the 0 - 3 cm length class) are widely distributed and have been sampled from St. Lucia in the north east to the Klein river in the south west. This suggests that spawning is also widespread.

Acanthopagrus berda

Catches during 1969 were much better than during 1970 and 1971. Data for the latter two years have therefore been lumped in the presentation of the results.

Length at recruitment

No specimens were caught in the plankton or box nets but some recruitment takes place at a very early stage in the life cycle because specimens as small as 10mm were sampled in estuaries. However the results show that such small specimens are uncommon as they were recorded in 1969 but not in 1970 or 1971 (Figs.46 and 47). Normally the smallest specimens seem to belong to the 2 - 3cm length class and most recruitment takes place in the length range 3 - 5cm.

Month of onset and duration of recruitment

The results obtained in 1969 show that estuarine recruitment started in July and that it continued until as late as December, when specimens in the 3 - 4cm length class were still well represented in the catch and were apparently migrating into estuaries. During 1970 and 1971 recruitment was first detected in August and specimens less than 5cm were not recorded after November. Estuarine recruitment thus seems to be somewhat variable and extends over a period of 4 - 6 months.

Rate of growth of juvenile recruits

It is difficult to obtain a reliable estimate from these data. Catches from July to December 1969 were made in the drag net which has a narrow selectivity range and does not catch specimens of more than 5 - 6cm efficiently as they tend to swim too fast to be surrounded by the net. The modal series is thus biased by the net selectivity. However the January 1970/71 catch was taken in a variety of gear and if its mode (85mm) is generally representative of 0-group juveniles (Fig.47), and is related to the modal size of 15mm for the first recruits in July 1969 (Fig.46), an estimated monthly growth increment of 11.7mm is obtained. An additional estimate of 10mm per month can be calculated from the September to December catches (Fig.47) which were taken in a number of different types of gear. It seems probable that these estimates approximate the actual growth rate of juvenile <u>A. berda</u>.

Occurrence in South African estuaries

The data indicate (Table 13) that juveniles are almost entirely restricted to Natal and are distinctly sub-tropical in distribution.

<u>Argyrosomus</u> <u>hololepidotus</u>

Almost the entire catch was taken in the commercial shrimp trawl operated in Potters Channel, St. Lucia (locality shown in Fig.3). As can be seen from Fig.48, catches were markedly seasonal and it therefore appears that the population is migratory, with few juveniles actually living and maturing in the Potters Channel area. This is thought to take place in the deeper parts of the lake (where they have been caught in small mesh gill nets) and not in the marginal shallows where few specimens have been caught despite extensive netting with various types of gear.

Length at recruitment

Because catches have only been made in the shrimp trawl it is important to examine the selectivity characteristics of this net before drawing conclusions regarding the actual length at first recruitment. Comparison of fish girth dimensions with mesh size has shown that specimens of less than 8cm can escape through the mesh but that this becomes more difficult as length increases. Consequently net selectivity is likely to be partly responsible for the poor catches of 5 - 8cm specimens. Nevertheless it is considered doubtful whether extensive estuarine recruitment occurs in this length range for if this took place one would have expected more individuals to become entangled with the prawns and other fish caught during the approximately 2 550 hours of trawling from which data have been obtained.

Catches indicate that recruitment starts at about 5cm and is most intensive within the length range of about 8 - 15cm. Larger specimens were caught less frequently but this could be because they are fast enough to evade the net. Considerable numbers of these specimens probably also enter estuarine systems.

Month of onset and duration of recruitment

During the 1970/71 season (Fig.48) the inward migration started in October, was most intense from November to February and declined during March and April. The following season a few recruits were recorded in September, the period of greatest intensity of recruitment stretched from October to February, and the decline again took place during March and April. There is clearly a spring/summer migration of juvenile kob into St. Lucia and this can also be expected to occur in other Natal estuaries.

Rate of growth of juvenile recruits

Although the catches (Fig.48) indicate a progressive increase in fish size, they do not form a well defined modal series suitable for obtaining a reliable estimate of growth. This is because the population in Potters Channel is migratory, has a fairly wide length range and is only sampled in reasonable numbers during four months of the year.

Occurrence in South African estuaries

Juveniles have only been recorded in St. Lucia, Richards Bay and the Keiskamma estuary in the Eastern Cape (Table 13). However, experience in St. Lucia showed that they tended to prefer deeper parts of the system and were not susceptible to capture in the drag and seine nets which are most effective in the estuarine shallows. This probably accounts for the poor catches taken in other estuaries.

Liza macrolepis

Length at recruitment

Plankton and box net catches failed to reveal the presence of larvae in Natal estuaries, the smallest juveniles encountered being 14mm in length. The larval stage of the life cycle seems to occur at sea. Scoop netting in the shallows yielded large numbers of fry in the 1 - 2cm length class and it appears that this is the minimum size at which estuarine recruitment takes place (Figs.49 and 50). Extensive migration into estuaries occurs amongst specimens 2 - 4cm in length and probably also amongst specimens of 4 - 5cm.

Month of onset and duration of recruitment

From Figs. 49 and 50 it is apparent that very small specimens (1 - 2cm length class) first start entering estuaries in May and continue to do so until September, after which they still occur but become rare. Larger specimens (2 - 4cm) were abundant from September to December, and although many of these could have entered estuaries earlier and at a smaller size, it seems probable that active recruitment takes place during these months. The relatively small catches in January, February and March show that some small specimens still occur during this period.

Although annual variation might be partly responsible for the prolonged occurrence of these small fish (the data cover three years), it is nevertheless clear that recruitment takes place over an extended period. It appears to be most intense during the six months July to December.

Occurrence in South African estuaries

Specimens of 2 - 6cm have been recorded from Delagoa Bay and from the Quissico lakes which are located about 300km further north in Mozambique. This indicates that juveniles are likely to occur in tropical East Coast estuaries and that their distribution extends southwards into South African waters.

Table 13 shows that juveniles have been sampled in most estuaries between the Kosi lakes and the Xora River in the Transkei. Further to the south they occur less frequently and none have been obtained beyond the Keurbooms river. In South Africa it is evident that juvenile *L. macrolepis* are primarily sub-tropical in distribution.

Liza dumerili

Length at recruitment

Larvae were not caught in the plankton or box nets and very small fry in the 1 - 2cm length class were only obtained in St. Lucia estuary in scoop nets during August and September 1971 (Fig.51). This length class was not encountered in other estuaries, so extensive recruitment of these very small specimens seems unlikely. Specimens in the length range 2 - 5cm were only recorded in small numbers despite the fact that similar sized juveniles of other species were caught in abundance in the same sampling gear. As selectivity characteristics are likely to be very similar for all juvenile mullet, the poor catch is considered to show a genuine scarcity of these length classes in Natal estuaries.

Larger specimens of about 5 - 8cm were relatively abundant and it appears that most recruitment takes place within this length range. This is considerably larger than in the case of the other mullet species studied.

Month of onset and duration of recruitment

Recruitment of specimens of less than 5cm occurs mainly from August to February. Larger specimens apparently spend this period at sea and move into estuaries from January to June.

Occurrence in South African estuaries

Very small juveniles of 0 - 3cm have been recorded between the St. Lucia lakes and the Swartkops river, while larger specimens (3 - 12cm) have been sampled on the South Coast as far west as the Breede river (Table 13). It seems probable that this approximates the limit of their distribution because Talbot (1955) did not sample this species in the Klein river.

It is apparent that juvenile L. dumerili utilise both sub-tropical and warm temperate estuaries in South Africa. Spawning is also likely to be widespread.

Valamugil buchanani

Length at recruitment

No larvae were collected in the plankton or box nets and this stage of the life cycle is considered to occur at sea. Only three specimens in the 2 - 3cm length class were caught in estuaries, but specimens of 3 - 5cm are abundant (Fig.52). This can be regarded as approximating the range of major recruitment. Inward migration of larger juveniles is also likely to take place.

Month of onset and duration of recruitment

Fry of less than 5cm have been sampled over a long period (Fig.52) but it must be borne in mind that these data were obtained over three years and consequently include annual variations in the period of recruitment. Examination of the catches for individual years and of the number of juveniles netted, shows that recruitment occurs mainly during the months February to July (only in 1969 were specimens obtained during October).

During 1972 juveniles of the above length range were found to be abundant in the inshore environment from April to June. Specimens were sampled with scoop nets in the vicinity of the groynes and shark nets along the Durban beachfront. Juveniles of other species of mullet have not been recorded in these areas.

Occurrence in South African estuaries

Fry of less than 3cm are rare (see above) but specimens of 3 - 12cm have been recorded between St. Lucia and Xora river (Table 13). They appear to be mainly sub-tropical in distribution.

Valamugil cunnesius

Length range and duration of recruitment

No larvae were caught in the plankton or box nets and this stage if the life cycle is presumed to occur at sea. Fry in the length classes 2 - 5cm seem to occur erratically and in relatively small numbers in Natal estuaries. The best catches were recorded in January, February and March 1970, but during the same months the following year no specimens were captured despite much increased sampling effort. Juveniles in the length range 5 - 8cm also seem to occur in relatively small numbers (Fig.53) but larger specimens of 8 - 15cm are somewhat more abundant.

These results suggest that juveniles do not utilize the estuarine environment of the region nearly as much as those of several other species of mullet. No definite season of immigration is apparent and even specimens of less than 5cm have been recorded over a nine month period (October to June).

Occurrence in South African estuaries

Juveniles appear to be entirely subtropical in distribution as they have only been obtained in Natal between St. Lucia and Durban Bay (Table 13). It seems probable that they occur further north in the estuaries of Mozambique.

Elops machnata

Small catches of juveniles were made (Table 16) despite the fact that this species is very abundant in the St. Lucia system. Since spawning occurs at sea (Section 7.2.2.2) immigration must take place but this was not detected in the gill nets or the shrimp trawl used in the

Narrows. Furthermore, as all but 10 of the 113 juveniles recorded were netted in the northern parts of St. Lucia, it is apparent that migration through the south lake also went undetected.

The explanation seems to be provided by the small number of leptocephalid-like organisms of 2 - 4cm caught in the lake. These fit Smith's (1949, p.85) description of the early stages of life of the family Elopidae: 'The newly hatched young is quite unlike the adult, being transparent and ribbon-like, but changes rapidly with growth'. As the specimens sampled had well developed upper and lower caudal fins and were therefore not eel larvae, it seems very likely that they did belong to the Elopidae. As only two species of this family occur in local estuaries, and one (Megalops cyprinoides) is rare in St. Lucia, it is considered highly probable that the larvae represent the recruitment phase of E. machnata. The explanation for their being sampled in such small numbers is probably that they are too small to be captured in the Potters Channel shrimp trawl, and that they prefer the deeper parts of the lake and were not very susceptible to capture in the drag, seine and scoop nets that were used extensively in the marginal shallows.

Myxus capensis

It can be seen from Table 17 that small numbers of specimens of 2 - 5cm have been recorded during the months August to December. This pattern is similar to that of the common mullet species of the Natal region and suggests that M. capensis also spawns in local waters.

Juveniles less than 12cm in length have been sampled between St. Lucia and Knysna (Table 14).

Pomadasys hasta

Most specimens were caught in the Potters Channel shrimp trawl and relatively few in the juvenile seine and drag nets that are operated in the marginal shallows of St. Lucia lake. This suggests that the species favours the deeper parts of the system. Interpretation of the data (Table 18) is complicated by the fact that gear selectivity has influenced the length composition of the catch, only one of the specimens of less than 7cm having been caught in the shrimp trawl. It appears that use of this gear leads to underestimation of the proportion of juveniles of 4 - 7cm due to its selectivity characteristics, whilst the other nets catch relatively few specimens due to the species' habitat preferences. Recruitment of 4 - 7cm juveniles is therefore likely to take place more extensively than the data indicate.

Juvenile P. hasta appear to be sub-tropical in distribution as they have only been recorded in Natal estuaries (Table 14).

Therapon jarbua

The 1 - 2cm length class is the smallest recorded in estuaries (Table 19) and included a number of fry 12mm in length. Catches were made in open water at night with the plankton and box nets as well as in the scoop and seine nets in the marginal shallows. As specimens less than 12mm were not recorded in estuaries, it appears that early larval life occurs at sea. However, estuarine recruitment obviously takes place at an early stage and is likely to be more extensive than the catches indicate because many small specimens were seen escaping through the mesh of the seine and drag nets.

Juveniles in the length range 1 - 3cm have been netted from November to May and this appears to be the main recruitment period for this species.

It is evident from Table 14 that juveniles are sub-tropical in distribution as they have only been recorded from Natal and Transkei estuaries.

Thryssa vitrirostris

A total of 110 specimens were sampled (Table 20). Of these only three were in the 1 - 2cm length class while 20 were 2 - 3cm in length. Estuarine recruitment seems to start within this length range.

The low incidence of very small specimens tends to confirm the conclusion based on plankton net catches (Section 7.2.2.4) that the ripe running adults recorded in St. Lucia (Section 7.2.2.2) failed to produce viable young.

Miscellaneous species

Ellochelon luciae

As only 29 specimens have been recorded (length 3 - 19cm) this species is considered to be rare.

Gerres acinaces)
Gerres oyena)
Gerres punctatus)

Juveniles of these species are fairly common in the Kosi lakes which are located on the northern boundary of Natal. Their distribution is sub-tropical (and probably also tropical), the Natal and northern Transkei coasts being near the limits of their range (Table 14).

Hypacanthus amia

Juveniles are rare in Natal estuaries but become more common towards the south west where they have been sampled in the Transkei and as far as the Kromme river (Table 14). They probably extend somewhat further west than these data indicate.

Lithognathus lithognathus

Juveniles were not recorded in Natal or Transkei estuaries in the course of the present survey and appear to occur mainly in the Cape East and South Coast region (Table 14).

Liza richardsoni

No juveniles have been recorded in Natal or Transkei estuaries during the course of this survey (Table 14). They were first encountered in the Kwelera estuary (near East London), became increasingly abundant towards the south west and were the only mullet juveniles obtained in the Berg river on the Cape West Coast.

Liza tricuspidens

Very few juveniles have been recorded in Natal estuaries despite the fact that there is evidence that adults spawn at sea in this region. Juveniles are common in the Transkei (Table 14) and become increasingly abundant further toward the south west.

Rhabdosargus globiceps

Juveniles of this species were recorded between the Kromme and Breede rivers. Talbot (1955) reports their presence in the Klein river west of Cape Agulhas.

8.3.3 Habitat preferences

Juvenile fishes generally favour those parts of estuaries which support the growth of marginal and submerged aquatic vegetation. This affords them shelter and

and protection from predators as well as an enriched feeding regime. Although they do not feed directly on this vegetation, it provides a substrate for the growth of large numbers of epiphytes, especially algae and diatoms, which are grazed extensively by fish such as mullet and by invertebrate herbivores. The importance of this has been emphasised by Wood *et al* (1969) who report that the biomass of epiphytes is often comparable to that of the 'sea grasses' on which they grow. Another very important influence of macrophytic vegetation on feeding arises from the organic detritus which it produces and which fulfils a vital function in the estuarine trophic web. The micro-organisms which decompose detritus, together with its breakdown products, provide food for a great variety of animals of which crustacea and bivalve molluscs are the most important (Day, 1951; *inter alia*). These in turn are eaten by fishes. From the above it can be readily understood why the vegetated estuarine margins and shallows in the vicinity of banks and islands support a greater diversity of fish species, and quantitatively larger populations, than bare sandy areas or the deeper muddy bottoms generally found toward the middle of bays and lagoons.

The marginal vegetation in many tropical and subtropical estuaries includes mangroves and this is also true of the East Coast of South Africa where they extend nearly as far south as the Kei river. The importance of the typical shallow pools, creeks and backwaters in the lives of juvenile fish and prawns has been mentioned by many workers. Routine sampling in Richards Bay in the vicinity of the mangroves south of Spinach Point (Fig.5) has shown that juveniles of the following fishes favour this area: *A. berda*, *A. hololepidotus*, *J. belengerii*, *P. indicus* and *V. cunnesius.* These species are not restricted to mangrove areas and also occur elsewhere, apparently favouring muddy substrates.

Underwater observations have shown that juvenile fish shelter amongst mangroves, particularly the aerial roots of *Avicennia*. These often extend about midway down the tidal range and form dense underwater 'forests' along estuarine margins where they tend to penetrate to within a short distance of the sea and are consequently encountered by juveniles soon after they enter the estuarine environment. As soon as danger threatens fish fry dart into the haven provided by the roots and have been seen to remain in close proximity to them while moving into estuaries with the tide.

A fairly narrow band of eel grass (*Zostera capensis*) is typically found between the mangroves and the tidal channels and provides shelter at a deeper level where it plays an increasingly important role towards low tide when the mangroves are exposed. *Zostera* tends to become more prolific and to form extensive 'beds' some distance into estuaries where tidal currents are not so strong and where more extensive shallows occur. Its influence on productivity has been highlighted by Wood *et al* (1969) and its importance stressed by Day and his co-workers in their various ecological surveys of South African estuaries. The results of the present programme confirm that these eel grass beds are particularly favoured by juvenile fishes and show that they support a greater variety of species and larger populations than any other estuarine habitat. Juveniles regularly netted in abundance in these areas include: *L. equulus*, *L. dumerili*, *L. macrolepis*, *M. cephalus*, *P. commersonni*, *R. holubi*, *R. sarba* and *T. jarbua*. These are juveniles of the most important estuarine angling and food fishes of Natal.

Other aquatic macrophytes which become important as salinities decrease and which play similar roles in the biology of juvenile fishes are *Ruppia* spp. and *Potomegeton pectonatus*. Marginal vegetation in the form of reeds (*Phragmites australis*) and sedges (*Scirpis* sp.) becomes more prolific as salinities decrease and often extends for considerable distances into the estuarine shallows. Juvenile fishes abound in these areas.

Mention should also be made of the open, deeper waters of estuaries which tend to have muddy bottoms and where certain species are characteristically found. These include: A. hololepidotus, J. belengerii, L. equulus, P. hasta, S. bleekeri and T. vitrirostris. Although population density may not be as great as in the habitats mentioned above, these open waters occupy large areas in the bigger estuarine systems such as St. Lucia and Richards Bay and can be expected to support considerable populations of these species.

To conclude this section special mention should be made of the occurrence of juvenile fishes in the St. Lucia lake system under the hypersaline conditions prevalent during the research period. The salinity tolerances of juveniles were found to be very similar to those of adults, most of the important species being able to tolerate levels in excess of 65°/₀₀ (Fig.9).

Probably the most adverse effect caused by the hypersaline regime was the death of the submerged macrophytic and marginal vegetation (the latter only survived above lake level and in the few localised areas on the eastern shore of the lake where there was freshwater seepage). From what has already been discussed it is clear that this must have had serious consequences for the juvenile fauna and it seems inevitable that the populations were much reduced in size during this period. Nevertheless good catches were made along parts of the eastern shore where plant detritus tended to accumulate in small bays, backwaters and channels. (In one such area a 4½ minute haul of the juvenile seine net yielded juveniles of 13 species and included 523 P. commersonni, 207 R. sarba and 83 R. holubi). This detritus was not produced by what might be considered 'normal' estuarine processes but consisted of terrestrial vegetation grazed by hippo and voided in their tracks leading down to the lake, in their wallows along the water's edge and in the lake where they spend most of the day. Showers of rain ensure that much of this finds its way into the lake. As between 430 - 450 hippo are resident on the eastern shores (Natal Parks Board game count records), it is apparent that they were able to make a substantial contribution to the basic detritus level in the food chain and to play an important role in maintaining the lake as a juvenile fish nursery during this period of hypersalinity.

Under normal conditions when there is a prolific growth of aquatic vegetation the contribution of hippo would tend to be less important. However it is interesting to ponder the fact that before the advent of European hunters much larger populations inhabited St. Lucia. Some insight into the numbers that must have been present is obtained from Finlay (1903) who states that a hunting party killed 150 hippos at the lake in 1853 and that in the same year John Dunn killed 203 'sea cows' during a three month visit to the area. From this it is clear that hippos must in the past have played a more important role in the ecology of this system than is the case today. Furthermore, as hippo occurred all the way to the south western Cape (Sclater, 1900), and were 'often found in brackish estuaries', the 'mouths of African rivers being a favourite resort of theirs' (Bryden and Buckley, as quoted by Shortridge, 1934), it can be concluded that these animals formerly formed an integral part of the ecology of most East and South Coast estuaries. The complexity of ecological systems is amply demonstrated by this relationship between one of Africa's largest terrestrial herbivores, the estuarine food web, juvenile fishes and ultimately their adult marine populations.

8.4 Discussion

Mention has been made of the fact that the estuarine fish fauna of Natal includes the juveniles of 20 angling species and an additional 10 species which are valuable as human food. Many of these migrate into estuaries at a very small size. Figure 54 shows that species such as M. cephalus, A. berda, R. holubi and L. macrolepis first appear at lengths of less than 2cm, and together with R. sarba and V. buchanani, complete their most active estuarine recruitment phase by the time a length of about 5cm is attained. P. commersonni continues to migrate into estuaries until it reaches about 7cm, while most active immigration occurs in L. dumerili and A. hololepidotus over the length ranges 5 - 8cm and 8 - 15cm respectively. Figure 55 shows that an additional 20 species start entering estuaries at lengths of between 1 - 6cm. These facts serve to emphasise the juvenile nursery function of Natal estuaries.

A similar occurrence of juvenile fishes ranging in length from less than 2cm has been reported by Munro (1945) for Australian estuaries in southern Queensland and New South Wales. Adults of species such as Acanthopagrus australis and Rhabdosargus sarba are reported to spawn near estuary mouths from where their larvae and post-larvae become washed passively into estuaries by the tides. Nair (1957 a, b) also reports that this occurs in Mugil cephalus and Ambassis gymnocephalus in the Kayamkulam lake in southern India. However neither of these workers expresses an opinion on the quantitative importance of this passive transport or makes any attempt to relate it to the active immigration of larger specimens.

Larval and post-larval fishes must also be washed into South African estuaries by tidal action, particularly in species such as A. berda, L. dumerili and L. macrolepis which have been found to spawn in the vicinity of estuary mouths (Section 7.2.2). However plankton netting in St. Lucia estuary yielded very few larval fishes (Section 7.2.2.4) and available evidence suggests that active estuarine recruitment of slightly larger fry is quantitatively much more important in East Coast estuaries.

The role of marginal vegetation and of submerged macrophytes in the biology of juvenile fishes has already been stressed in Section 8.3.3. Munro (1945) also draws attention to the importance of these areas and states that after leaving the plankton fish fry congregate in nursery grounds amongst the Zostera weed growth of shallow flats and brackish creeks. Wood et al (1969, p.496) record that 'the fish population of a number of coastal lagoons fell away sadly when Zostera was removed by a change in the environment'. The conclusion which must be drawn from this evidence is that the nursery function of estuaries is intimately related to the viability of plant communities. (Attention has already been drawn (Section 8.3.3) to the 'special case' represented by the hypersaline St. Lucia lake where hippo continued to supply organic detritus to the system after the death of the aquatic plant communities and thus helped to maintain the juvenile nursery function).

The seasonality of the immigration of juveniles into Natal estuaries is of considerable interest. Its main features can best be described by reference to the species for which most comprehensive data have been obtained. From Fig.56a it is apparent that six species start entering estuaries in winter (June to August) and complete their main periods of immigration by the end of spring (November) or start of summer (December). Limited recruitment of four of these continues during summer but this generally involves larger specimens than the winter/spring period (details in Figs. 39,40 (March 1972 catch taken in Durban Bay), 43 and 44/45).

Three species in Fig.56a do not conform to the above pattern. A. hololepidotus enters estuaries during spring and summer, while L. dumerili does so during summer and autumn. Reference to Fig.54 shows that both species recruit at a larger size than the others. Although little is known about the reproductive biology of A. hololepidotus, it has been established that L. dumerili spawns at the same time as the other species (June to November; Fig.36). From this it can be deduced that the differences between the recruitment of this and the other species arise because its juveniles spend longer at sea before they migrate into estuaries. V. buchanani also deviates from the main pattern mentioned above, small juveniles of 3 - 5cm having been recorded (mainly in St. Lucia and Richards Bay) during late summer, autumn and winter. The reason may be that this species is less dependent on estuaries and its biology has not developed so as to maximise the utilisation of this environment by its juvenile stages. This possibility is indicated by the fact that its juveniles have been sampled in smaller numbers in estuaries than those of the main group above, and in contrast to all other mullet species, have been recorded in abundance in the inshore zone.

Comparison of Fig.56b (derived from Fig.56a) with Fig.56c reveals an interesting relationship between the number of species that migrate into estuaries each month and mean monthly river flow. It is apparent that most recruitment takes place during the winter when river outflow is at a minimum and during spring when it increases at the start of the wet season. During the summer rainfall period of maximum river outflow the number of species that enter estuaries becomes reduced and larger length classes tend to be involved. The extent of summer recruitment into narrow estuaries with high outflow velocities is unknown but is likely to be much less than in the large systems like Richards Bay and St. Lucia lake where most of the data reported above were obtained.

Many East Coast estuaries become isolated from the sea during the dry season owing to the formation of sandbars across their mouths. In spring lagoon levels rise due to increased river flow (Fig.56c) and the overtopping of sandbars by the equinoctial tides (Fig.56b). As a result estuary mouths open, the fish that were isolated during the dry season are released to sea and recruitment of the next generation of juveniles is able to begin. This generally takes place somewhat later in the year than in open systems and varies annually in accordance with the onset of the spring rains.

Quantitative estimates of the number of juveniles that move into East Coast estuaries have not been made but an indication that large numbers are involved is obtained from research conducted by Blaber (1973b) in the Kleinemond estuary on the south east coast (indicated in Fig.2). An estimated 55 000 juvenile <u>R. holubi</u> entered this small system (18km long, mainly 60m - 130m wide) while it was open to the sea from September to December 1970. Due to a high mortality rate only 11 000 returned to sea when the mouth re-opened seven months later. The following year a smaller population estimated at 13 000 individuals entered the system but on this occasion mortalities were low and about the same number returned to sea.

If it is taken into account that Kleinemond is but one small system and that the Transkei and Natal coasts are characterised by a high frequency of estuaries (see Section 2.3), many of which are much larger in size, it is apparent that literally millions of juveniles are likely to invade this total estuarine area. Notwithstanding high mortality rates, large numbers must survive and return to sea to supplement the marine stocks.

8.5 Summary and Conclusion

1. Juveniles of 54 species of fish have been recorded in Natal estuaries. Of these, twenty are angling species and ten non-angling species valuable as human food.
2. Most of the species in Natal estuaries are sub-tropical in distribution with the result that their abundance declines towards the south west. Juveniles generally

have a more restricted range than adults.

3. Juveniles of species such as L. dumerili, M. cephalus and R. holubi occur in estuaries along the whole of the East and South Coasts. Juveniles of certain South Coast species do not extend into Natal estuaries.

4. Estimates of early growth rates have been made for M. cephalus, P. commersonni, R. sarba, R. holubi and A. berda.

5. Shallow areas that support marginal and submerged aquatic vegetation form particularly favourable habitats for juvenile fishes and play a major role in the function of estuaries as fish nurseries.

6. Habitat preferences of numerous species are described.

7. The influence of hypersaline conditions on the juvenile fish fauna and the ecological role of hippo in maintaining the nursery function of St. Lucia lake are discussed.

8. Attention is drawn to the fact that juveniles of a number of important species start migrating into Natal estuaries at lengths of less than 2cm and complete their most active recruitment phase by the time a length of 5cm is attained. An additional 21 species start entering estuaries at lengths of between 1 - 6cm.

9. In open estuaries most immigration takes place during winter and spring when river outflow is at a minimum and begins to increase at the start of the wet season.

10. In blind estuaries recruitment usually starts during spring when increased river flow forces open estuary mouths.

11. Evidence is presented to show that very large numbers of juveniles utilise the estuarine environment and then return to sea to supplement the marine stocks.

9. GENERAL DISCUSSION

Detailed discussions of the different aspects of biology studied in this programme have already been given in Sections 5.4, 6.4, 7.4 and 8.4. The object of this general discussion has consequently been restricted to highlighting the main features of the biology and ecology of the fish fauna, to assessing the extent of its dependence on estuaries and its probable status in the light of exploitation and environmental degradation.

9.1 Main features of the biology and ecology of the estuarine fish fauna

The estuarine fish fauna of the East Coast of South Africa is composed of more than 110 euryhaline species. Most of these are sub-tropical Indo-Pacific forms, some are South Coast endemics, while cosmopolitan and temperate-eastern-Atlantic species are also included in the fauna.

The limits of distribution of many of these species fall along the East Coast and are related to the gradual decline in water temperature towards the south west. However these limits vary seasonally and enable sub-tropical species to extend into the South Coast region during summer and more temperate fishes to occur in Natal waters during winter. These shifts in distribution are probably assisted by the south west flowing Agulhas Current and to some extent by the poorly understood inshore Counter Current that flows in the opposite direction.

The main feature of the life cycles of most species is the division into a juvenile phase which is largely estuarine and an adult phase which is primarily marine. The adult populations occur on the continental shelf and only a relatively small proportion enters estuaries. This usually takes place seasonally at the time of the year when there is a movement of adults into the inshore spawning grounds. Fish in pre-spawning and partially spawned condition tend to move in and out of the lower reaches of estuaries with the tides, while post-spawners generally extend further into estuaries (particularly the larger systems) where they can spend several months before returning to sea. During this period they must benefit considerably from the rich feeding regime typical of the estuarine environment.

Another feature of the biology of this fauna is that most species breed at sea; only a few small specialised forms having adapted their entire life cycles to the variable conditions of temperature, salinity and turbidity characteristic of estuaries. Marine sampling has revealed that 13 species spawn in Natal inshore waters and of these three have been recorded in ripe running condition in the immediate vicinity of estuary mouths. In the species for which most comprehensive data are available (Fig.57) spawning has been found to last for 4 - 8 months and to take place during late autumn, winter, spring and to a limited extent at the beginning of summer. Comparison of spawning and recruitment periods (Fig.57) shows that there is a delay of 1 - 3 months before the offspring start migrating into estuaries. This generally takes place most actively for 4 - 6 months during winter and spring, thereafter declining in intensity during summer. Attention has already been drawn to the fact (Section 8.4) that this enables recruitment to occur when river outflow is at a minimum and when the increased flow in spring opens the mouths of blind lagoons making them available to colonisation by juveniles. It has also been suggested (Section 7.4) that the prolonged spawning and recruitment seasons have a 'buffering' action against failure of recruitment as a result of adverse climatic conditions.

On the basis of the evidence outlined above it can be postulated that the migration to inshore spawning grounds and the timing and duration of spawning constitute a reproductive mechanism which enables juveniles to make maximum use of East Coast estuaries. To establish whether this mechanism is likely to be effective it is necessary to review what is known about the inshore current systems of Natal and to assess whether physical conditions are conducive to the retention of juvenile stages in inshore waters.

Most of the research on inshore currents has been undertaken as a basis for the planning of effluent outfalls into the sea and the new port at Richards Bay. It has been found that the water mass between the Agulhas Current and the shore moves parallel to the coast and reverses its direction at intervals of 1 - 3 days under the influence of the atmospheric low pressure systems which move through the area from the south west. Overall movement of water is slow (0.01 - 0.1m/sec) and generally occurs in a northerly direction (Oliff and Addison, 1970). In the vicinity of Richards Bay (Fig.58) the frequency and strength of the northgoing current is greatest inshore (recording station located 800m from the beach) and declines with distance from the coast due to the increasing influence of the Agulhas Current (Russell, 1972; Zwamborn, 1972; Pearce 1973). Further to the north at Cape St. Lucia, the Agulhas Current impinges more directly on the coast and results in stronger inshore currents having a predominantly southgoing tendency, particularly during summer. However even at this time of the year reversals occur (recording station 800m offshore) and these northgoing currents have been shown to be more frequent during the winter (Oliff and Addison, 1970). Further inshore where the influence of the Agulhas Current is less pronounced a stronger northgoing tendency can be expected and it is likely that a 'tongue' of water moves around Cape St. Lucia from the south (Oliff, <u>pers</u>. <u>comm</u>.)

Onshore currents have been recorded on 10 - 50% of occasions, depending on locality. At the surface these are partly under the influence of wind, but on the seabed they result from an inshore movement of Agulhas Current water (from 30 - 50m depth), which causes continuous low intensity upwelling in the inshore zone. This is associated with an offshore displacement of water at 10m depth (Oliff and Addison, 1970; Pearce 1973).

The conclusion drawn from these studies is that the poorest exchange between inshore water and the Agulhas Current occurs in the area north of Durban and south of Cape St. Lucia (Fig.58) and that these conditions are not particularly good for the disposal of effluents. This is extremely interesting when applied to the reproduction of the fishes mentioned above because it indicates that the relatively passive fertilised egg and larval stages resulting from inshore spawning are unlikely to become lost to the Natal region by rapid incorporation into the Agulhas Current. This is reinforced by the probability that the duration of this phase is short. Breder and Rosen (1966) quote periods of 24 - 72 hours from fertilisation to hatching for species of Leiognathidae, Pomadasidae and for *Platycephalus indicus*; while Blaxter (1969) reports that larval life can be as little as a few days in tropical species and from a few weeks to months for temperate fishes. In sub-tropical forms it seems unlikely that larval life extends into months. Shehadeh and Norris (1972) state that *Mugil cephalus* larvae hatch 36 - 50 hours after fertilisation and that larval life lasts for 42 days, by which time a length of 17 - 18mm is attained. This length is greater than that of the smallest specimens recorded in Natal estuaries and therefore confirms the data in Fig.57 which show that recruitment begins about a month after the start of spawning. Although the ability of larval specimens to perform extensive migrations is likely to be limited, the possibility that they undertake diurnal vertical migrations in association with the plankton cannot be ignored as this could provide a mechanism for utilising the onshore components on the surface and the seabed to compensate for offshore tendencies such as that in the 10m depth range. Whether this actually takes place must, unfortunately, remain a matter of conjecture at this stage.

Available information on the characteristics of the inshore water mass thus indicate that current conditions in the Natal region are likely to be conducive to the retention of progeny resulting from inshore spawning. It therefore seems reasonable to conclude that the postulated reproductive mechanism would be effective. In addition, any active inshore migratory tendency on the part of juveniles would seem to have survival value and could have become established as an innate or 'instinctive' behaviour pattern during this phase of their lives.

In sub-tropical species such as A. berda, P. commersonni, R. sarba and V. cunnesius, the effective operation of these mechanisms would seem to be vital since juveniles would have little chance of survival if they became transported by the Agulhas Current into the much colder South Coast region during winter (when spawning occurs). This is unlikely to apply to species such as M. cephalus, L. dumerili and R. holubi which occur on both the East and South Coasts, but they can nevertheless be expected to benefit from being retained inshore because this permits earlier recruitment into estuaries where the feeding regime is more in keeping with their requirements than in the deep sea region of the Agulhas Current.

To conclude this discussion of the relationship between currents and the biology of estuarine fishes consideration will be given to the mechanisms likely to be responsible for the migration of juveniles into St. Lucia lake. The entrance to this system is located north of Cape St. Lucia where the continental shelf is only about 5km wide (Fig.58). Inshore spawning has been recorded in this area and might account for the smallest fry that enter the estuary. However the narrowness of the shelf and the currents that prevail make it unlikely that the mass of larger juveniles that enter the system originate from this limited inshore region. The other areas from which they can be derived are to the south where the continental shelf widens (and the inshore currents have already been described), and from the region 300km to the north where an extensive shelf occurs in the vicinity of Delagoa Bay. Little information is available about the currents in the latter but the configuration of the Bay and the coastline further north suggest that it is an area of slow water turnover. This, together with the fact that R. sarba has been found to spawn in the Bay near Inhaca Island, suggests that it is likely to be a spawning ground for a number of estuarine species. Transportation of their offspring to the vicinity of St. Lucia would appear to be dependent upon the south-going Agulhas Current because there are indications of an inshore northgoing counter current south of Delagoa Bay (Macnae and Kalk, 1969). There is also evidence of a counter current on the stretch of coast north of St. Lucia estuary where the turbid floodwaters of the Umfolosi river, and the sugar cane it washes into the sea, move northwards and at times extend beyond Sordwana Bay. In order to return inshore, juveniles would depend on active swimming, onshore current components and the eddies generated between the inner edge of the Agulhas Current and the shore. However the narrowness of the shelf and strong flow of this current in the region of St. Lucia would seem more likely to result in juveniles being swept past this area to the wider continental shelf slightly further south, than to favour large scale movement of juveniles into the vicinity of St. Lucia estuary. Furthermore, as the reproductive biology of these fishes seems to be adapted to keeping the young close to shore there might be a limited supply of potential recruits in the Agulhas Current. In view of these factors it is considered unlikely that southward movement of juveniles from the Delagoa Bay region constitutes the main mechanism responsible for recruitment into the St. Lucia lakes.

Available evidence indicates that juveniles are more likely to be derived from the southern spawning area. The northerly movement of inshore water in the vicinity of Richards Bay and around Cape St. Lucia has already been discussed and provides a mechanism for the transport of juvenile fishes. The fact that this northgoing tendency is more pronounced in winter is significant because it is during this time of the year that most species start migrating into estuaries. Additional evidence of recruitment from the south is provided by the species R. holubi, juveniles of which are abundant in St. Lucia but for which there are no records of either juveniles or adults further north in Kosi Bay, Delagoa Bay or elsewhere in Mozambique. Blaber (1973c) attributes this distribution pattern to temperature and states that temperatures in the tidal basin of Kosi estuary can exceed the lethal limits established for this species experimentally. These data suggest that the adult spawning populations of R. holubi are located south of St. Lucia and that recruitment takes place from here and not from the north. Clearly, if such a mechanism for juvenile recruitment exists for one species, it is also likely to apply to others.

Estuarine sampling has shown that vast numbers of juvenile fishes succeed in entering estuaries and in most species greatly exceed the number of adults in this environment. Juveniles of a total of 54 species have been recorded in Natal estuaries and of these 20 are angling species and 10 non-angling species of value as human food. Immigration takes place at a small size, 28 of the 30 species mentioned above having been recorded at lengths of less than 6cm.

A number of the most important of these start entering estuaries very early in life (at 1 - 2cm) and complete their most active recruitment phase by the time a length of about 5cm is attained. However, the length composition of catches in open estuaries and juvenile growth rates of *P. commersonni*, *R. holubi* and *R. sarba*, indicate that less than a year is generally spent in this environment before there is a return to sea in preparation for the adolescent and adult phases of life.

The pattern in 'blind' estuaries seems to be similar, immigration taking place during the spring/summer period when mouths open, and emigration at the start of the next spring when river outflow opens mouths once more. As most species can cope adequately with estuarine conditions it is unlikely that they are adversely affected by being temporarily 'trapped' in blind lagoons. In fact it is important not to underestimate the significance of these systems in the biology of estuarine fishes.

Habitat preferences within estuaries vary with species, but in general shallow areas rich in marginal and submerged aquatic vegetation support both a greater diversity and density of juvenile fishes than bare sands or deeper muddy-bottomed estuarine basins. This is largely attributable to the rich feeding regime provided by epiphytes growing on these plants and the invertebrate fauna associated with the detritus they produce. Protection from predators can also be expected to play a role. However research by Blaber (1973b) and the length composition of catches in the present programme indicate that mortalities can be high and are mainly caused by predatory fish and birds.

The main conclusions to be drawn from the above are that the biology of the estuarine fish fauna is adapted to the utilisation of both open and closed estuaries by juveniles, that this nursery function is most important during the first year of life, and is intimately related to the aquatic plant communities.

The fact that the total estuarine area of the East Coast supports very large numbers of juvenile fishes which return to sea and supplement marine stocks, has already been discussed (Section 8.4). A question which often arises is whether these species are wholly or only partly dependent upon an estuarine juvenile phase. This is extremely difficult to answer owing to the problems inherent in sampling juvenile fish populations which have different habitat preferences and are likely to be spread over an area as large as the continental shelf. As far as the author is aware no quantitative assessment and factually conclusive solution to this problem has been obtained anywhere in the world, and the East Coast of South Africa is no exception. Consequently an assessment has to be made on the basis of the circumstantial evidence which is available.

Only a relatively small proportion of the overall fish fauna of the East Coast is adapted physiologically to cope with estuarine conditions. It seems reasonable to assume that these species benefit from this specialisation and that their success depends to some extent upon it. The predominance of juveniles in estuaries suggests that it is the early phase in the life cycles for which this holds the greatest adaptive significance and survival value. In fact this seems to be of such importance that the reproductive biology of adults has become adapted (see earlier) so as to favour the utilisation of estuaries by juveniles. Although this in no way indicates that these species are totally dependent on estuaries, the inference which can be drawn is that their life cycles are closely associated with this environment and are in large measure dependent upon it. It can thus be stated that the future of these sport angling and food species is directly related to the viability of estuaries.

The danger of jeopardising estuarine dependent resources through mismanagement of the estuarine environment has been stressed for the Atlantic and Gulf coasts of the United States by Hedgepeth (1947); Springer and Woodburn (1960); Cain (1966); McHugh (1966); Gunter (1967); and many others. Sykes (1967) describes some interesting examples of how State authorities have legislated to protect estuarine areas, particularly vegetated nursery 'beds' which are held to be of paramount importance. An interesting fact is highlighted by de Sylva (1969), who points out that a sport fishery should not be assessed by the weight of the catch, but by the 'cost' of each kilogram caught. Thus in California it costs the angler $18.11 to catch one salmon, which is of 5½ times greater value to the economy than would be a similar fish in the commercial fishery. In 1965 the United States commercial fishery for estuarine dependent species was valued at $75 million, while the sport fishery for these species was valued at over $331 million. de Sylva (p.156) concludes that: 'The key to the future of marine sport fisheries resources is in the survival and management of our estuaries'. Pollard (1974) makes a similar plea for the protection of estuarine nurseries from ecological despoilation by man in order to safeguard the estuarine dependent commercial and sport fisheries of Eastern Australia.

In view of the above and the information which has become available from the present study, it is appropriate to conclude this discussion with a brief review of the status of the local fauna in relation to exploitation and to the condition of East Coast estuaries.

9.2 <u>The status of the estuarine fish fauna</u>

Commercial exploitation of estuarine fishes is very limited and consists mainly of line fishing and trawling of A. hololepidotus in Natal and Cape waters. However this species occurs over a wide area and depth range and available evidence suggests that it is not as estuarine dependent as many other species. With the present fragmentary knowledge of the marine populations it is impossible to comment on the status of these stocks.

Commercial beach seining takes place on Durban's Addington Beach and in the vicinity of Inhaca Island. Relatively small numbers of P. commersonni, R. sarba and M. cephalus are caught and it is unlikely that such localised operations have any impact on these species.

Sport angling is very popular on the East Coast and species such as P. commersonni, R. sarba, A. berda, E. machnata and A. hololepidotus are caught in estuaries as well as from sandy and rocky beaches. Additional species such as Lithognathus lithognathus and Hypacanthus amia are caught seasonally when they migrate into Transkei and Natal waters. Although no catch statistics are available for any of these species, the generally low intensity of fishing for them and the fact that large specimens are still plentiful, indicate that they are unlikely to be endangered at present levels of exploitation.

This is also considered to apply to non-angling food species. M. cephalus is seine netted for bait by the Natal Parks Board in Richards Bay and St. Lucia, but poaching in the latter probably results in a greater weight of fish being taken. Small mullet of a variety of species are caught in cast and drag nets for use as 'live' bait, but licenses for these nets are issued in limited numbers. Commercial shrimp catches taken in St. Lucia and Richards Bay by the Natal Parks Board include juvenile fishes but relatively small numbers are involved. In general the capture of juveniles is strictly controlled in Natal and this is also true of the Cape and the Transkei. The conclusion to be drawn is that there is no cause for concern over the present levels of exploitation of estuarine dependent species and that considerably greater catches could be taken.

However despite the relatively low levels of exploitation there is no room for complacency concerning the future of East Coast estuarine dependent resources. The deterioration of the estuarine environment of the region has already progressed so far that there is every probability that these stocks have become reduced. A brief review of the state of estuaries emphasises this point.

The hypersalinity problems of the St. Lucia lake system and the decline in its fauna during these periods have already been described (Sections 3.3.1 and 4.3). Since this is South Africa's largest estuarine system any decline in its viability can be expected to have serious consequences. The conversion of half of Richards Bay into a bulk carrier port and the decline in the former biological wealth of Durban Bay owing to city and harbour development, have also been mentioned (Sections 3.3.2 and 3.3.3). Estuaries at the mouths of the major rivers of Natal and the Transkei have been devastated by siltation resulting from agricultural mismanagement in their catchments. Unfortunately this is also true of many of the smaller blind estuaries on the Natal coast which have become so shallow that they are almost completely drained when their mouths open to the sea. Without the retention capacity provided by deeper channels and pools, most of the juvenile fishes that enter on the flood tide move back to sea with the ebb and recruitment is consequently reduced. Moreover, the increasing practice of digging open sandbars to prevent the inundation of sugar cane lands and holiday plots (which should not be permitted to encroach on estuarine and riverine margins) also has deleterious consequences. Not only are juveniles released to sea prematurely, but because mouths do not scour fully, they remain open for shorter periods and limit the time available for re-colonisation. Whereas many of the changes to our estuaries are irreversible, this sort of mismanagement can be prevented. Some of the finest estuaries in South Africa are to be found in the Transkei where the smaller rivers are relatively unspoilt by siltation. However there is alarming evidence of destruction of indigenous forests and cultivation of excessively steep slopes which will need to be stopped if degradation of the valuable resource represented by these estuaries is to be avoided.

This brief resume only touches on some of the factors responsible for the decline in South African estuaries. However it serves to draw attention to the vulnerability of the estuarine environment to mismanagement on land. Failure to recognise the close interrelationship between terrestrial, estuarine and marine ecosystems often leads to practices such as river pollution and destruction of wetlands (e.g. by roads, agriculture and industry) in the course of development. All too often these activities are justified without it being realised that they are detrimental to the equally important tourist industry and living marine resources forming the basis of commercial and sport fisheries.

Despite the decline in viability of South African estuaries and the threat posed by the increasing tempo of development, there is hope for the future. The responsible attitude of the Government is exemplified in the development of Richards Bay where considerable expense is being incurred in establishing the part not required for harbour development as an estuarine sanctuary with a separate mouth to the sea. The Natal Parks Board at present controls the unspoilt Kosi lakes on the northern border and is actively involved in improving the management of the St. Lucia lake system. Steps are also being taken by this Board and the Cape Department of Nature Conservation to implement fisheries legislation which includes the restriction of the use of small mesh nets, capture of undersize fish and the protection of bait organisms. However, in view of the value of the sport fishery to the economy, its recreational potential and the ever increasing demand for animal protein, the author feels compelled to make a plea for increased efforts in the field of estuarine conservation. While the attention being paid to the larger systems is to be applauded, sight should not be lost of the important role of the many small estuaries on the East and South Coasts in maintaining the viability of estuarine dependent resources.

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Species*†	Distribution						Standard Common Name*	Number (Smith 1949)
	Steno-haline	Euryhaline				Fresh-water		
		R	C	VC	A			
Abudefduf saxatilis (Linn.)	+						Sergeant major	761
Abudefduf sordidus (Forssk.)	+						Spot damsel	760
Acanthopagrus berda (Forssk.)				+			Riverbream	707
Acanthopagrus bifasciatus (Forssk.)	+						Twobar bream	706
Acanthurus fulgiginosus (Lesson)	+						Dusky surgeon	611
Acanthurus lineolatus (Linn.)	+						Tailring surgeon	609
Acanthurus triostegus (Linn.)	+						Convict surgeon	608
Acentrogobius caverensis Bleeker	+						Weeper	931
Albula vulpes (Linn.)		+					Bonefish	99
Alectis ciliaris (Bloch)		+					Threadfin mirrorfish	527
Alectis indicus (Ruppell)	+						Indian mirrorfish	528
Allanetta klunzingeri Smith		+					Slender silverside	892
Alutera monoceros (Osbeck)	+						Unicorn leatherjacket	1152
Amanses pardalis Ruppell	+						Honeycombed filefish	1144
Ambassis commersoni Cuv. in C.&V.			+				Banded glassy	636
Ambassis gymnocephalus (Lacep.)			+				Glassy	637
Ambassis natalensis Gilch. & Thomp.					+		Slender glassy	634
Ambassis productus Guichenot				+			Longspine glassy	635
Amblyrhynchotes honckeni (Bloch)	+						Evileyed blaasop	1198
Anguilla mossambica (Peters)		+						1094
Anthias squamipinnis (Peters)	+						Sea goldie	459
Antennarius striatus (Shaw)	+						Striped angler	1240
Antennarius pinniceps Valenc.	+							1239
Antennablennius bifilum (Gunth.)	+						Horned rockskipper	967
Apogon fraenatus Val.	+						Spurcheek cardinal	484
Argyrosomus hololepidotus (Lacep.)					+		Kob	552
Arothron aerostaticus (Jenyns)	+						Plainfin blaasop	1206
Arothron hispidus (Lacep.)		+					White-spotted blaasop	1207
Arothron immaculatus (Bloch)			+				Blackedged blaasop	1203
Arothron nigropunctatus (Bloch)	+						Blackspotted blaasop	1204

Table 1. Checklist of fishes recorded in Natal estuaries, including their distribution, relative abundance and common names (R=rare, C=common, VC=very common, A=abundant). *Scientific and common names according to Smith and Jackson (in press). †Scientific names of mullet according to Thomson (in press).

Species	Distribution						Standard Common Name	Number (Smith 1949)
	Steno-haline	Euryhaline				Fresh-water		
		R	C	VC	A			
Atractoscion aequidens (Cuv.)	+						Geelbeck	554
Bathygobius fuscus Ruppell	+						Frill goby	910
Blennius steindachneri Day	+						Maned blenny	950
Blennius fascigula Barnard	+						Ringnecked blenny	951
Bothus myriaster (Tem. & Schl.)	+						Disc flounder	316
Bothus pantherinus (Ruppell)	+						Leopard flounder	317
Carangoides ciliaris Ruppell	+						Longfin kingfish	390
Carangoides crysophrys (Cuv.)	+						Longnose kingfish	516
Carangoides djedaba (Forssk.)		+					Slender yellowtail kingfish	508
Carangoides fulvoguttatus (Forssk.)	+						Yellow spotted king-fish	522
Carangoides melampygus (Cuv.)		+					Bluefin kingfish	513
Caranx dentex (Bl-Schn.)	+						Underjaw kingfish	507
Caranx dinema Bleeker	+						Shadow kingfish	519
Caranx ferdau (Forssk.)	+						Ferdy kingfish	523
Caranx ignobilis (Forssk.)		+					Giant kingfish	520
Caranx mate (Cuv.)		+					Finlet kingfish	510
Caranx sexfasciatus Q.&G.		+					Bigeye kingfish	511
Carcharhinus limbatus (M.&H.)	+						Blacktip shark	5
Carcharhinus leucas (M.&H.)			+				Zambezi shark	9
Cephalopholis argus (Schneider)	+						Peacock rockcod	425
Chaetodon auriga Forssk.	+						Threadfin butterfly-fish	592
Chaetodon mertensii Cuv. in C.&V.	+						Pearly butterflyfish	603
Chaetodon kleinii Bloch	+						Whitespotted butter-flyfish	600
Chaetodon lunula (Lacep.)	+						Halfmoon butterfly-fish	598
Chaetodon vagabundus Linn.	+						Vagabond butterfly-fish	599

Table 1. (Continued)

Species	Distribution						Standard Common Name	Number (Smith 1949)
	Steno-haline	Euryhaline				Fresh-water		
		R	C	VC	A			
Chanos chanos (Forssk.)			+				Milkfish	105
Cheimerius nufar (Val.)	+						Santer	740
Chelondon patoca (Hamilton)			+				Milkspotted blaasop	1201
Chromis dimidiatus (Klunz.)	+						Apartheid	746A
Cirrhithchys aprinus (Cuv.)	+						Spotted hawkfish	393
Clarias gariepinus (Burchell)						+	Barbel (Crass, 1964)	-
Coracinus multifasciatus (Pellegr.)	+						Banded galjoen	645
Crenidens crenidens (Forssk.)		+					Karanteen	732
Dascyllus trimaculatus (Ruppell)	+						Domino	751
Dasyatis brevicaudatus (Hutton)	+						Short-tailed stingray	81
Dasyatis jenkinsii (Annandale)	+						Sharpnose stingray	80B
Dasyatis pastinacus (Linn.)	+						Blue stingray	80
Dasyatis thetidis (Waite)	+						Thorntail stingray	79A
Dasyatis varnak (Forssk.)		+					Honeycomb stingray	79
Dinoperca petersii (Day)	+						Lampfish	454
Diplodus sargus Linn.		+					Blacktail	713
Drepane punctata (Linn.)		+					Concertinafish	576
Echeneis naucrates Linn.	+						Shark remora	949
Echidna nebulosa (Ahl)	+						Floral moray	1122
Eleotris fusca (Bloch)			+				Dusky sleeper	938
Elops machnata Forssk.				+			Springer	100
Engraulis capensis (Gilch.)		+					Cape anchovy	123
Enneapterygius obtusirostre Klunz.	+						Lowcrest triplefin	1007
Epinephelus andersoni Boul.		+					Catface rockcod	437
Epinephelus areolatus (Forssk.)	+						Squaretailed rockcod	446
Epinephelus diacanthus (Val.)	+						Twospine rockcod	443
Epinephelus fario (Thunberg)	+						Trout rockcod	444
Epinephelus guaza (Linn.)	+						Yellowbelly rockcod	435
Epinephelus tauvina (Forssk.)		+					Bullnose bass	447
Fistularia petimba Lacep.	+						Smooth flutemouth	361

Table 1. (Continued)

Species	Distribution						Standard Common Name	Number (Smith 1949)
	Steno-haline	Euryhaline				Fresh-water		
		R	C	VC	A			
Formio niger (Bloch)	+						False butterfish	500
Gaterin niger (Cuv.)		+					Harry hotlips	690
Gaterin plagiodesmus (Fowler)	+						Barred rubberlip	691
Gaterin schotaf (Forssk.)		+					Minstrel	-
Gerres acinaces Bleeker			+				Smallscales pursemouth	631
Gerres oblongus Cuv.		+					Oblong pursemouth	633
Gerres oyena (Forssk.)			+				Slenderspined pursemouth	629
Gerres punctatus Cuv.		+					Threadfin pursemouth	628
Gerres rappi (Barnard)		+					Evenfin pursemouth	632
Gilchristella aestuarius (Gilch. & Thomp.)					+		Estuarine round-herring	108
Glossogobius giuris Hamilton			+				Tank toby	919
Gobius acutipennis (Cuv.)			+				Sharptailed goby	923
Gobius nebulosus (Forssk.)			+				Shadow goby	917
Gobius nudiceps Cuv.			+				Barehead goby	927
Gymnura natalensis (Gilch.)	+						Backwater butterflyray	86
Haplochromis philander (M. Weber)						+	Mouthbreeder (Crass, 1964)	-
Hemiramphus far Forssk.		+					Spotted halfbeak	222
Heniochus acuminatus (Linn.)	+						Coachman	590
Hepsetia breviceps Cuv.		+					Cape silverside	893
Herklotsichthys punctata (Ruppell)							Onespot herring	111
Hilsa kelee (Cuv.)			+				Kelee shad	109
Hypacanthus amia (Linn.)		+					Leervis	539
Hyporhamphus delagoae (Bernard)		+					Delagoa halfbeak	220
Hyporhamphus improvisus (Smith)			+				Shortfin halfbeak	217
Hyporhamphus knysnaensis (Smith)				+			Knysna halfbeak	218
Istiblennius edentulus (Bloch)	+						Rippled rockskipper	971
Johnius belengerii (Cuv.)			+				Mini-kob	549

Species	Distribution						Standard Common Name	Number (Smith 1949)
	Steno-haline	Euryhaline				Fresh-water		
		R	C	VC	A			
Kuhlia rupestris (Lacep.)	+						Rock flagtail	413
Kuhlia taeniurus Cuv.	+						Barred flagtail	412
Labroides dimidiatus (Val.)	+						Blue streak cleaner wrasse	805
Lactoria cornuta (Linn.)	+						Longhorned cowfish	1178
Leiognathus equulus (Forssk.)				+			Slimy	626
Lepidopus caudatus (Euphrasen)	+						Scabbardfish	867
Leptoscarus vaigiensis (Q.&G.)	+						Marbled parrotfish	826
Lethrinus nebulosus (Forssk.)	+						Blue emperor	702
Lithognathus mormyrus (Linn.)	+						Sandsteenbras	727
Liza alata (Steindachner)		+					Diamond mullet	881
Liza dumerili (Steindachner)					+		Groovy mullet	884
Liza macrolepis A. Smith					+		Largescaled mullet	886
Liza richardsoni (Smith)		+					Southern mullet	887
Liza tricuspidens (Smith)		+					Striped mullet	882
Liza vaigiensis (Q.&G.)		+					Squaretailed mullet	883
Lobotes surinamensis (Bloch)		+					Tripletail	414
Lutjanus argentimaculatus (Forssk.)		+					River snapper	664
Lutjanus fulviflamma (Forssk.)			+				Dory snapper	659
Lutjanus russellii (Bleeker)	+						Russell snapper	660
Lutjanus vaigiensis (Q.&G.)	+						Yellow striped snapper	669
Lycodontis undulatus (Lacep.)	+						Leopard moray	1129
Megalaspis cordyla (Linn.)	+						Torpedo kingfish	534
Megalops cyprinoides (Broussonet)		+					Oxeye tarpon	101
Monodactylus argenteus (Linn.)			+				Moony	581
Monodactylus falciformis Lacep.			+				Cape moony	580
Mugil cephalus Linn.					+		Grey mullet	877
Muraenesox cinereus (Forssk.)		+					Pike conger	1117
Mustelus canis (Mitchell)	+						Plain smoothhound	19

Table 1. (Continued)

Species	Distribution						Standard Common Name	Number (Smith 1949)
	Steno-haline	Euryhaline				Fresh-water		
		R	C	VC	A			
Myliobatis aquila (Linn.)	+						Eagleray	76
Myxus capensis (Valen.)			+				Freshwater mullet	890
Neoscorpis lithophilis (Gilch. & Thomp.)	+						Stonebream	646
Odontaspis taurus Rafinesque	+						Spotted ragged-tooth shark	25
Omobranchus banditus Smith	+						Bandit blenny	955
Ophisurus serpens (Linn.)	+						Sandsnake-eel	1106
Oplegnathus conwayi Richardson	+						Cape knifejaw	461
Osbeckia scripta (Osbeck)	+						Scribbled leather-jacket	1153
Ostracion tuberculatus Linn.	+						Boxy	1177
Otolithes ruber (Schneider)			+				Snapper kob	553
Parachaeturichthys polynema Bleeker	+						Taileye goby	920
Parapercis nebulosa Q.&G.	+						Barfaced sandsmelt	381
Paraplagusia bilineata (Bleeker)	+						Twolined tonguefish	335
Pelates quadrilineatus (Bloch)			+				Trumpeter	402
Periopthalmus koelreuter africanus Eggert			+				African mudhopper	936A
Pisodonophis boro (Ham.-Buch.)		+					Giant snake-eel	1100
Platax pinnatus (Linn.)	+						Batfish	577
Platycephalus crocodilus Tilesius	+						Crocodile flathead	1064
Platycephalus indicus (Linn.)			+				Bartailed flathead	1063
Platycephalus tentaculatus Ruppell	+						Tentacled flathead	1066
Plotosus anguillaris (Bloch)	+						Eel-catfish	163
Polydactylus plebeius (Brouss.)	+						Striped threadfin	898
Polydactylus sextarius Bloch		+					Sixfinger threadfin	900
Pomacanthodes striatus (Ruppell)	+						Old woman	583
Pomadasys commersonni (Lacep.)					+		Spotted grunter	679
Pomadasys gouraka Russell	+						Indian grunter	674
Pomadasys hasta Bloch			+				Javelin grunter	676
Pomadasys maculatum Bloch	+						Saddle grunter	677

Table 1. (Continued)

Species	Distribution						Standard Common Name	Number (Smith 1949)
	Steno-haline	Euryhaline				Fresh-water		
		R	C	VC	A			
Pomadasys multimaculatum (Playfair)		+					Cock grunter	678
Pomadasys olivaceum Day	+						Piggy	675
Pomatomus saltatrix (Linn.)		+					Elf	547
Pranesus pinguis (Lacep.)	+						Hardyhead silverside	894
Pristis pectinatus Latham			+				Largetooth sawfish	59
Promicrops lanceolatus (Bloch)		+					Brindle bass	452
Psammogobius knysnaensis Smith			+				Knysna sandgoby	906
Psenes whiteleggi Waite	+						Shadow driftfish	853
Pseudorhombus arsius (Hamilton)		+					Largetooth flounder	304
Pterois volitans (Linn.)	+						Devil firefish	1047
Rastrelliger brachysoma (Bleeker)	+						Spotlight mackerel	838
Rastrelliger kanagurta (Russell)	+						Longjawed mackerel	837
Regalecus glesne (Ascanius)	+						Oarfish	263
Rhabdosargus holubi Steindechner				+			Cape stumpnose	709
Rhabdosargus sarba (Forssk.)					+		Natal stumpnose	710
Rhabdosargus thorpei Smith		+					Bigeye stumpnose	-
Rhinecanthus aculeatus (Linn.)	+						Blackbar triggerfish	1169
Rhinoptera javanica M.&H.	+						Flapnose ray	77A
Sardinella gibbosa (Bleeker)	+						Goldstripe sardinelle	114
Sarpa salpa (Linn.)	+						Strepie	731
Sauvagella madagascariensis (Sauvage)		+						110
Scarus ghobban tarssk.	+						Blue parrotfish	824
Scomberoides commersonianus Lacep.			+				Largemouth queenfish	546
Scomberoides lysan (Forssk.)		+					Queenfish	545
Scomberoides tala (C.&V.)			+				Tala queenfish	544
Scomberomorus commerson (Lacep.)	+						King mackerel	840
Scomberomorus leopardus (Shaw)	+						Spotted mackerel	841
Sebastapistes oglinus Smith	+						Fingertip scorpionfish	1035
Secutor insidiator (Bloch)		+					Slender soapy	625
Secutor ruconius (Buch.-Ham.)	+						Soapy	624

Table 1. (Continued)

Species	Distribution						Standard Common Name	Number (Smith, 1949)
	Stenohaline	Euryhaline				Freshwater		
		R	C	VC	A			
Siganus oramin (Schneider)		+					Double-eyed rabbitfish	901
Siganus rivulatus (Forssk.)		+					Mottled rabbitfish	902
Sillago sihama (Forssk.)		+					Silver smelt	467
Solea bleekeri Boulenger					+		Blackhand sole	328
Sphyraena barracuda (Walbaum)		+					Great barracuda	896G
Sphyraena jello Cuv.		+					Pickhandle barracuda	895
Sphyraena flavicauda Ruppell		+					Yellowstripe barracuda	897
Stephanolepis auratus (Castelnau)		+					Porky	1140
Stigmatogobius dewaali (Weber)			+				Checked goby	918
Stigmatogobius durbanensis (Barnard)		+					Durban goby	915
Stolephorus commersoni (Lacep.)			+				Tropical anchovy	119
Syngnathus acus Linn.		+					Longnosed pipefish	350
Syngnathus cyanospilus Bleeker		+					Bluespot pipefish	351
Syngnathus djarong Bleeker			+				Belly pipefish	352A
Syngnathus spicifer Ruppell		+					Belly barred pipefish	352
Synodus indicus (Day)	+						Indian lizardfish	172
Taenioides esquivel Smith	+						Bearded eelgoby	904
Terapon jarbua (Forssk.)			+				Thornfish	401
Thalassoma lunare (Linn.)	+						Crescent-tail wrasse	777
Thryssa setirostris (Brouss.)		+					Longjawed glassnose	122
Thryssa vitrirostris (Gilch. & Thomp.)					+		Orangemouth glassnose	121
Thyrsoidea macrura (Bleeker)		+					Slender giant moray	1123
Tilapia mossambica Peters						+	Largemouth tilapia (Crass, 1964)	-
Torpedo sinus-persici Olfers	+						Marbled electric ray	91
Trachinotus blochii (Lacep.)		+					Tropical pompano	542
Trichiurus lepturus Linn.		+					Atlantic cutlassfish	869
Tripterodon orbis Playfair	+						Spadefish	578
Trypauchen microcephalus Bleeker			+				Comb goby	937

Table 1. (Continued)

Species	Distribution						Standard Common Name	Number (Smith 1949)
	Steno-haline	Euryhaline				Fresh-water		
		R	C	VC	A			
Tylosurus crocodilus (Lesueur)		+					Crocodile needlefish	229
Tylosurus leiurus (Bleeker)		+					Needlefish	228
Upeneus vittatus (Forssk.)	+						Yellowstriped goatfish	561
Uropterygius concolor (Ruppell)	+						Liniform reef-eel	1133
Valamugil buchanani (Bleeker)			+				Bluetail mullet	888
Valamugil cunnesius (Valenc.)				+			Longarm mullet	879
Zanclus cornutus (Linn.)	+						Moorish idol	618

Table 1. (Continued)

Months	St. Lucia South Lake Mean	St. Lucia South Lake Range	St. Lucia Estuary Mean	St. Lucia Estuary Range
J	27.0^{6}	22.0 - 30.5	25.1^{3}	22.0 - 27.5
F	25.9^{6}	22.0 - 29.0	25.9^{7}	23.0 - 27.5
M	24.7^{4}	21.0 - 28.0	24.6^{6}	21.0 - 28.0
A	24.6^{5}	21.5 - 26.0	23.8^{5}	22.5 - 25.0
M	21.1^{6}	17.5 - 23.5	21.5^{4}	19.0 - 24.0
J	17.7^{3}	16.5 - 20.0	19.5^{6}	16.0 - 21.8
Jl	19.6^{3}	18.0 - 21.0	19.8^{5}	18.0 - 21.0
A	19.7^{5}	18.0 - 21.0	20.5^{4}	18.0 - 23.5
S	20.7^{1}	20.0 - 21.5	21.0^{4}	17.5 - 22.5
O	20.2^{5}	18.5 - 22.0	20.6^{6}	18.0 - 27.5
N	25.0^{3}	24.0 - 26.2	23.1^{3}	22.0 - 24.0
D	26.8^{4}	25.2 - 29.0	27.4^{3}	24.5 - 30.00
Summer D,J,F.	26.6^{16}	22.0 - 30.5	26.1^{13}	22.0 - 30.0
Autumn M,A,M.	23.5^{15}	17.5 - 28.0	23.3^{15}	19.0 - 28.0
Winter J,Jl,A.	19.0^{11}	16.5 - 21.0	19.9^{15}	16.0 - 23.5
Spring S,O,N.	22.0^{9}	18.5 - 26.2	21.6^{13}	17.5 - 27.5

Table 2. Water temperatures (°C) recorded (1969 and 1970) by immersing maximum/minimum thermometers with gill nets (at depth of 45cm below the water surface) for duration of netting periods. Superscript indicates number of periods on which means are based.

Species	Total length to standard length	Total length to fork length
M. cephalus	$Y = -1.3256 + 0.7628X$	$Y = 1.1152 + 0.8877X$
P. commersonni	$Y = -7.4938 + 0.7803X$	$Y = -2.1901 + 0.9252X$
R. sarba	$Y = -2.1796 + 0.7297X$	$Y = -3.0993 + 0.8898X$

Table 3a: Regression equations for conversion of total length to standard and fork length.

SPECIES	ENVIRONMENT	LENGTH CLASSES (10CM) 0	10	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170	NO. IN SAMPLE	ABUNDANCE * JUVS.	ADULTS	COMMENTS
CARANX IGNOBILIS	ESTUARINE %	82.8	8.6	3.5	3.5	1.7														58	R	R	JUVENILES OCCUR IN ESTUARIES, BUT SPECIES MAINLY MARINE; VERY COMMON IN AND JUST BEYOND SURF ZONE.
	MARINE N			2	7	2	3	1	3		1	1	1							21			
HYPACANTHUS AMIA	ESTUARINE %	3.5	1.2	9.2	17.2	20.7	17.2	4.6	4.6	4.6	13.8	3.5								87	R	R	MORE COMMON TO THE SOUTH IN CAPE ESTUARIES. SEASONALLY ABUNDANT IN WINTER AND EARLY SPRING; CAUGHT IN AND JUST BEYOND SURF ZONE.
	MARINE %							1.8	5.4	34.0	42.9	12.5	3.6							56			
MURAENESOX CINEREUS	ESTUARINE N								2	2	1	2	4	5	4	4				29	-	R	MAINLY MARINE, COMMON ON TUGELA BANK IN 30-40 M.
	MARINE N											2								2			

SPECIES	ENVIRONMENT	LENGTH CLASSES (4CM) 0	4	8	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68	72	NO. IN SAMPLE	ABUNDANCE JUVS.	ADULTS	COMMENTS
CARANX SEXFASCIATUS	ESTUARINE %		24.4	10.5	3.5	10.5	16.8	7.0	20.0	2.3	2.3	2.3	1.2								86	R	R	JUVENILES OCCUR IN ESTUARIES, BUT SPECIES MAINLY MARINE; COMMON IN AND JUST BEYOND SURF ZONE.
	MARINE N								1		2	1	1	1	2	2	1				11			
CHANOS CHANOS	ESTUARINE %			3.5	12.1	36.2	1.7	19.0	5.2	6.9	3.5	6.9	3.5								58	R	C	
LIZA ALATA	ESTUARINE %		6.6	1.3	3.9	6.6	3.9	6.6	2.6	5.3	1.3	3.9	14.0	17.1	11.8	6.6	3.9				76	R	R	APPEARS TO BE RARE IN NATAL WATERS.
LIZA TRICUSPIDENS	ESTUARINE %	7.0	2.0			1.0				2.0	9.0	11.0	22.0	22.0	15.0	9.0					100	R	R	MORE COMMON TO THE SOUTH IN CAPE ESTUARIES. ADULTS CAUGHT BY ANGLERS IN SURF ZONE.
	MARINE N									1	1	5	8	8	2	1	1				27			
MYXUS CAPENSIS	ESTUARINE %	87.2	5.8					2.3		3.5	1.2										86	C	R	APPEARS TO BE RARE IN NATAL WATERS.
OTOLITHES RUBER	ESTUARINE N						1	1	4	9	6	4	1								26	-	R	MAINLY MARINE; COMMON IN SURF ZONE, TRAWLED ON TUGELA BANK 30-40 M; ABUNDANT AND EXPLOITED COMMERCIALLY IN DELAGOA BAY.
	MARINE %					1.0	8.0	41.0	23.0	15.0	8.0	4.0	1.1								101			
PLATYCEPHALUS INDICUS	ESTUARINE %			3.1	2.3	3.1	3.1	4.6	9.2	9.2	13.7	12.2	13.7	13.7	6.9	2.3	3.1				131	R	C	
POMADASYS HASTA	ESTUARINE %	0.4	8.8	45.7	13.0	13.4	12.6	1.1	1.6	0.4	0.7	0.7	1.0	0.4		0.2	0.2				554	C	R	MAINLY MARINE; TRAWLED ON TUGELA BANK 30-40 M, LINE FISHED FROM SHORE AND ON REEFS DOWN TO 70 M.
	MARINE N				2	10	2				1										15			
VALAMUGIL BUCHANANI	ESTUARINE %	14.6	29.4	25.5	5.0	1.1	1.1	3.0	5.4	6.0	2.7	2.2	2.2	1.1	0.8	0.9	0.4	0.2	0.2		1332	VC	R	MAINLY JUVENILES IN ESTUARIES; ADULTS COMMON INSHORE

TABLE 3B. LENGTH COMPOSITION OF CATCHES FROM NATAL ESTUARINE AND MARINE ENVIRONMENTS WITH COMMENTS ON RELATIVE ABUNDANCE AND DISTRIBUTION. (CONTINUED OVERLEAF).

* A = ABUNDANT, VC = VERY COMMON, C = COMMON, R = RARE. THESE ESTIMATES HAVE BEEN MADE TO FACILITATE INTERSPECIFIC COMPARISONS OF THE RELATIVE ABUNDANCE OF JUVENILES, AND SEPARATELY, OF ADULTS. THE RATING GIVEN TO THE JUVENILE PHASE OF A SPECIES BEARS NO RELATION TO THAT GIVEN ITS ADULT PHASE. INTRASPECIFIC COMPARISONS CANNOT, THEREFORE, BE MADE.

SPECIES	ENVIRONMENT		LENGTH CLASSES (2CM) 0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	NO. IN SAMPLE	ABUNDANCE JUVS.	ADULTS	COMMENTS
AMBASSIS NATALENSIS	ESTUARINE	%	8.2	3.4	48.3	36.1	4.1																147	A	A	ABUNDANT THROUGHOUT LENGTH RANGE AS IT SPAWNS IN ESTUARIES.
AMBASSIS PRODUCTUS	ESTUARINE	%			1.8		1.8	29.0	23.6	27.3	7.3	9.1											55	C	VC	FAVOURS LOW SALINITY ESTUARIES.
GERRES ACINACES	ESTUARINE	%		2.8	43.3	27.9	9.7	3.6	4.1	4.5	0.8	0.4		0.4		1.6	0.8						248	R	R	
GERRES OYENA	ESTUARINE	%			2.3		8.0	6.8	2.3	4.6	10.2	5.7	8.0	14.0	18.6	12.0	4.6	1.1					86	R	C	
GERRES PUNCTATUS	ESTUARINE	%			9.5	9.5	5.4	6.8	1.4	46.0	16.2		1.4		4.1								74	R	R	
GILCHRISTELLA AESTUARIUS	ESTUARINE	%	**	5	75	20																	80	A	A	ABUNDANT THROUGHOUT LENGTH RANGE AS IT SPAWNS IN ESTUARIES.
HILSA KELEE	ESTUARINE	%		3.5	7.4	2.0	2.0	1.5	0.5	0.5	3.0	8.4	3.0	6.4	7.9	4.0	18.8	25.3	5.5	0.5			202	R	C	SHALLOW MARINE SPECIES; ABUNDANT AND EXPLOITED COMMERCIALLY IN DELAGOA BAY.
HYPORHAMPHUS KNYSNAENSIS	ESTUARINE	%	**		1.2	16.2	46.0	17.4	10.6	8.7													161	A	A	ABUNDANT THROUGHOUT LENGTH RANGE AS IT SPAWNS IN ESTUARIES.
JOHNIUS BELENGERII	ESTUARINE	%		0.3	1.0	2.8	0.9	2.3	2.1	2.4	17.0	25.2	11.7	17.4	13.7	3.3							702	C	VC	MAINLY MARINE; TRAWLED ON TUGELA BANK AND OFF ST. LUCIA MOUTH IN 30-40 M.
	MARINE	N							4	5	4	1											14			
LEIOGNATHUS EQUULUS	ESTUARINE	%	0.1	1.9	22.0	25.8	7.2	5.6	6.6	8.5	9.6	9.1	3.1	0.4									929	VC	VC	VERY COMMON AT SEA, TRAWLED OFF ST. LUCIA MOUTH IN 40 M.
	MARINE	N								10	20	7											37			
LUTIANUS FULVIFLAMMA	ESTUARINE	%		1.5	43.3	28.4	17.9	6.0				1.5							1.5				67	C	R	MAINLY MARINE, COMMON ON INSHORE REEFS.
SOLEA BLEEKERI	ESTUARINE	%		4.0	10.8	19.6	34.6	28.6	2.0	0.4													454	VC	A	ABUNDANT THROUGHOUT LENGTH RANGE AS IT SPAWNS IN ESTUARIES. TRAWLED OFF ST. LUCIA MOUTH IN 40 M.
	MARINE	N					3	9															12			
TERAPON JARBUA	ESTUARINE	%	7.5	7.9	25.6	21.6	20.8	6.4	3.5	1.8	3.3	0.7	0.4	0.4									453	C	C	SAMPLE UNDERESTIMATES ABUNDANCE OF ADULTS. TRAWLED OFF ST. LUCIA MOUTH IN 40 M.
	MARINE	N		2							1	5	2	2	3								15			
THRYSSA VITRIROSTRIS	ESTUARINE	%		0.4	1.9	5.7	13.1	15.8	4.0	6.6	23.0	14.8	12.6	2.1	0.1								1095	C	A	ABUNDANT IN ESTUARIES BUT MAINLY OCCURS IN DEPTHS OF 30-40 M.
VALAMUGIL CUNNESIUS	ESTUARINE	%		8.3	6.6	6.6	11.4	12.5	13.5	4.1	3.8	5.5	12.3	4.7	6.6	3.0	0.7						955	VC	VC	

TABLE 3B. (CONTINUED).

** PLANKTONIC STAGES NOT IDENTIFIED TO SPECIES.

Gill Nets	Month	Locality	Net hours	Salinity ($^{o}/oo$)	No. of fish netted	Length range (cm)
5cm Mesh	1969					
	March	South Lane Island	16.30	56.1	0	-
		West Bird Island	19.05	80.5	0	-
		Eastern False Bay	19.50	82.0	0	-
	July	Nyalazi River	16.15	46.5	1	31.0
	1970					
	February	Hells Gates	14.30	65.4	1	-
	March	Hells Gates	14.00	71.5	14	21.5-26.2
	May	Between Hells Gates and Fanies Island	17.30	60.8	42	23.4-31.7
7cm Mesh	1969	No netting				
	1970					
	February	Hells Gates	30.00	65.4	28	24.6-46.7
	March	Hells Gates	13.30	71.5	2	36.7-36.9
	May	Between Hells Gates and Fanies Island	15.30	60.8	49	29.0-51.0
		West Bird Island	23.15	83.5	0	-
9cm Mesh	1969					
	March	South Lane Island	16.25	56.1	2	37.0-38.3
		West Bird Island	19.00	80.5	0	-
		Eastern False Bay	19.50	82.0	0	-
	April	West Lane Island	20.00	47.0	16	41.2-66.8
	July	Nyalazi river	16.30	46.5	8	42.7-50.0
	1970					
	February	Hells Gates	15.00	65.4	29	40.3-62.5
	March	Hells Gates	13.35	71.5	9	38.7-56.0
	May	Between Hells Gates and Fanies Island	15.25	60.8	154	38.8-63.8
13cm Mesh	1969					
	March	South Lane Island	32.40	56.1	0	-
		West Bird Island	37.50	80.5	0	-
		Eastern False Bay	39.20	82.0	0	-
	April	West Lane Island	60.50	47.0	14	49.3-67.2
	1970					
	February	Hells Gates	15.00	65.4	9	48.7-65.7
	March	Hells Gates	13.30	71.5	3	52.2-54.0
Scoop Net	1970					
	January	Mkuze River Mouth	-	60.4	68	8.6-17.4
Throw Net	1970					
	February	Mkuze River Mouth	-	53.5	16	13.5-16.7

Table 4. Summary of gill net catches of *M. cephalus* in the north lake and the associated salinity conditions.

Month	Locality	Salinity °/oo	Comments
1969			
February	Fanies Island	53.6 }	
	Tewate	67.3 }	Abundant.
	South Lane Island	70.0 }	
	Hells Gates	78.0	One dead specimen
	(Hells Gates to False Bay	78.0 - 83.0	No evidence of any fish life).
	Distribution suggests southward movement to avoid lethal salinities.		
March	North Fanies Island	53.3	Abundant.
	Hells Gates	75.6	One dead specimen.
April	North Fanies Island	44.2 }	Heavy rains caused drop in salinity, mullet moved north away from low salinities of 20 - 25°/oo.
	South Lane Island	47.0 }	
	Lister Point	47.0	Mullet reappeared within one week of drop in salinity from 75°/oo.
May	Fanies Island	36.3 }	Small shoals.
	Lane Island	48.4 }	
June	Mkuze River	39.4	
	Lister Point	49.3	
July	Nyalazi River	46.5	
November	South Lane Island	48.0	
1970			
January	North Hells Gates	58.0	Abundant.
	Mkuze River	60.4	Abundant.
February	Mkuze River	53.5	
	Hells Gates	65.4	Abundant.
March	North Fanies Island	62.0	
	(Hells Gates northwards	77.0 - 86.0	No evidence of any fish life).
April	North Fanies Island	60.0	
May	North Fanies Island	75.6	
	North Hells Gates	81.0	
June	Lane Island	75.0	
July	Lane Island	80.0	
August	South Fanies Island	66.0	
	South Lane Island	84.0	Small specimens, species identification uncertain.
	North west Lane Island	86.0	Present.
October	Hells Gates	76.0	

Table 5. Summary of sightings of M. cephalus in the north lake and the associated salinity conditions.

Species	J	F	M	A	M	J	J	A	S	O	N	D	Reproductive Condition and Migrations
	Period of abundance in estuaries												
A. berda			—	—	—	—	—						Moves in and out of estuaries during spawning season; gonads mainly in post-spawning condition but some pre-spawners also occur.
A. hololepidotus				- -	- -	- -	- -	—	—	—			Direction of migrations poorly understood; some spent fish migrate into St. Lucia from June to October but most migrating specimens are reproductively inactive.
M. cephalus				—	—	—	—	—					Migrates out of St. Lucia lake in pre-spawning condition; pre- and post-spawners move in and out of estuaries; very few post-spawners return to St. Lucia lake.
L. macrolepis							—	—	—	—	—		Migrates out of St. Lucia lake in pre-spawning condition; pre- and post-spawners move in and out of estuaries, post-spawners return to St. Lucia lake.
L. dumerili							—	—	—	—	—		Migrates out of St. Lucia lake in pre-spawning condition; pre- and post-spawners move in and out of estuaries; post-spawners return to St. Lucia lake.
P. commersonni	—	—						—	—	—	—	—	Migrates into estuaries and St. Lucia lake in post-spawning condition from August onwards; returns to sea towards end of period of abundance.

Species	J	F	M	A	M	J	J	A	S	O	N	D	Reproductive Condition and Migrations
	Period of abundance inshore												
M. cephalus				—	—	—	—	—					Abundant during spawning season; migration of pre-spawners from estuaries only partly accounts for concentrations of mullet inshore, source of others unknown.
A. hololepidotus				—	—	—	—	—	—	—			Mainly inactive, some late spents do occur; migrates north eastwards along coast from cooler waters of the Cape and then returns again.
L. macrolepis						—	—	—	—	—	—		Abundant during spawning season; congregates on vicinity of estuary mouths and possibly in inshore zone.
L. dumerili						—	—	—	—	—	—		Abundant during spawning season; congregates in vicinity of estuary mouths and possibly in inshore zone.
R. sarba					—	—	—	—	—	—	—	—	Abundant during spawning and post-spawning period; not known where the fish that congregate inshore come from or disperse to.
P. commersonni	—								—	—	—	—	Abundant during spawning and post-spawning period; not known where the fish that congregate inshore come from or disperse to.

Table 6. Summary of periods of estuarine and inshore abundance, reproductive condition and migrations.

P. commersonni

	I	A	AR	R	RR	PS	S
January	24						1
April	31	2					
July	10						

N=68

R. sarba

	I	A	AR	R	RR	PS	S
January			No	sample			
April	32	7					7
July		5	2	1	21	6	4

N=85

Table 7. Gonad stages recorded from Inhaca Island, Mozambique (actual number of specimens plotted).

Species	Gonad Stage I	A	AR	R	RR	S	N	Comments
Drepane punctata	63		1			11	75	Spents sampled in October and November. Ripe running fish sampled in inshore marine environment during December, January and February.
Gerres oyena	30		1	1		10	42	
Gerres punctatus	24					7	31	
Hemiramphus far	17	2		1	1		20	Single female with translucent ova recorded in Richards Bay in December; spawning unlikely to occur in Natal estuaries.
Hypacanthus amia	8					17	25	Spents mainly from September to November.
Lutianus argentimaculatus	9	2				5	16	
Megalops cyprinoides	23					3	26	
Muranaesox cinereus	5	8	3	4		5	25	Spawning appears to occur in Spring and early Summer; but not in estuaries.
Platycephalus indicus	29			3	1	42	75	One ripe running female recorded in St. Lucia estuary in November but spawning not considered to be an estuarine function; spawning season during Spring and Summer.
Pomadasys multimaculatum	22					4	26	
Scomberoides commersonianus	8						8	
Tylosurus leirius	24	2		1	2	6	35	Two females with large translucent eggs (not actually running) recorded in Richards Bay and St. Lucia Lake during December and February.

Table 8. Frequency of occurrence of each stage of gonad development in the total estuarine catch of species that were sampled in relatively small numbers.

Species	Gonad Stage							N	Comments
	I	A	AR	R	RR	PS	S		
Ambassis natalensis	67	20	1	14	12	2	1	117	Ripe specimens recorded in August; and ripe running specimens in August, October and November. Some evidence of spawning in estuaries during late Winter and Spring.
Gilchristella aestuarius	5	3	0	8	33	0	0	49	Ripe specimens recorded in August and ripe running specimens in October. Evidence of spawning in estuaries during Spring.
Hyporhamphus knysnaensis	51	5	1	0	9	16	41	123	Ripe running and partially spawned specimens recorded in October, December and March. Some evidence of spawning in estuaries during warmer months of the year.
Therapon jarbua	18						1	19	No evidence of estuarine spawning.

Table 9. Frequency of occurrence of each stage of gonad development in the total estuarine catch of species that are abundant in Natal estuaries, but were sampled in relatively small numbers.

SPECIES	LENGTH CLASSES (5CM)																								N	COMMENTS
	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115		
ARGYROSOMUS HOLOLEPIDOTUS													1	3	4	2	8	8	7	11	9	5	4	1	63	SPECIES MAINLY INACTIVE IN NATAL WATERS.
			0	10	13	107	73	82	111	109	102	91	104	91	99	111	73	60	59	35	23	13	8	7	1381	LIMITED DATA AVAILABLE ON LENGTH AT MATURITY.
	LENGTH CLASSES (4CM)																									
	0	4	8	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68	72	76	80	84	88	92		
LIZA TRICUSPIDENS												1	12*	11	13	5									42	
										2	8	10	9	11	4	4									48	
PLATYCEPHALUS INDICUS								1	1	2	4	13*	14	12	6	3	3								59	
								1	8	9	13	3	4	8	3	-	1								50	
VALAMUGIL BUCHANANI									4	3	6	2	11*	5	3	8	4	2	1						49	
						2	5	24	33	52	34	21	19	11	8	5	1		1						216	
	LENGTH CLASSES (1CM)																									
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20					
AMBASSIS NATALENSIS						9*	13	19	3	1															45	LENGTH AT FIRST MATURITY HAS NOT BEEN DETERMINED DUE TO
					1	30	16	9	21	5															82	POOR SAMPLING OF ADOLESCENT LENGTH RANGE.
GILCHRISTELLA AESTUAREUS						3	25	16																	44	LENGTH AT FIRST MATURITY HAS NOT BEEN DETERMINED DUE TO
				1	2	2	2																		7	POOR SAMPLING OF ADOLESCENT LENGTH RANGE.
SOLEA BLEEKERI									4	6	18	34*	15	5	1	2									85	
					1	9	11	10	33	40	82	59	9	-	3										257	

TABLE 10. LENGTHS OF ATTAINMENT OF SEXUAL MATURITY. IN EACH LENGTH CLASS THE NUMBER OF SEXUALLY MATURE (UPPER ROW FIGURES) AND IMMATURE/INACTIVE FISH HAS BEEN LISTED. SEXES ARE LUMPED. (CONTINUED OVERLEAF).

* DESIGNATES THE LENGTH CLASS FROM WHICH ALL INACTIVE FISH WERE CONSIDERED TO BE SEXUALLY MATURE IN THE ANALYSIS OF THE GONAD CYCLE.

SPECIES	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	N	COMMENTS
ACANTHOPAGRUS BERDA								2	3	12	20*	23	29	21	16	15	27	14	3	5	1				191	
							4	4	10	18	16	19	12	13	15	9	7	7							134	
HILSA KELEE										5	3	2	13*	9	22	33	7								94	
						1			4	10	2	3	3	3	13	15	4	1							59	
HYPORHAMPHUS KNYSNAENSIS				2	30*	21	8	10																	71	
			1	19	29	7	7	2																	65	
JOHNIUS BELENGERII						1	4	6	42	80*	55	102	69	16											375	
					1	1	6	10	61	80	26	17	21	6											229	
LEIOGNATHUS EQUULUS						1	6	26	53*	38	14	1													139	
		1	10	39	9	19	41	60	43	59	17	3													301	
OTOLITHES RUBER												3	8	9*	5	4	15	7	8	3	5	3	3		73	LENGTH AT FIRST MATURITY HAS NOT BEEN DETERMINED DUE TO POOR SAMPLING OF ADOLESCENT LENGTH RANGE
										1	1	3	5	8	5	1		2		3					29	
RHABDOSARGUS HOLUBI									5	13*	13	12	8	12	3	4	3	2	2						65	LENGTH AT FIRST MATURITY HAS NOT BEEN DETERMINED DUE TO POOR SAMPLING OF ADOLESCENT LENGTH RANGE. DAY AND MORGANS (1956) ESTIMATE LENGTH AT MATURITY AS 15 CM.
								5	12	30	15	8	4	4	1										79	
THRYSSA VITRIROSTRIS				14	41	182*	23	53	212	128	120	17	1												791	LENGTH AT FIRST MATURITY HAS NOT BEEN DETERMINED DUE TO POOR SAMPLING OF ADOLESCENT LENGTH RANGE.
				6	21	40	4	10	18	25	22	5													151	
VALAMUGIL CUNNESIUS									2	21	65*	29	25	12	4		1								159	LENGTH AT FIRST MATURITY HAS NOT BEEN DETERMINED DUE TO POOR SAMPLING OF ADOLESCENT LENGTH RANGE.
									1	10	21	6	4	1											43	

LENGTH CLASSES (2CM)

TABLE 10. (CONTINUED).

* DESIGNATES THE LENGTH CLASS FROM WHICH ALL INACTIVE FISH

Species	In estuaries	In vicinity of estuary mouths	In marine inshore environment	In shallow water on continental shelf	In marine environment (details unknown)	Comments
Acanthopagrus berda		+				
Liza dumerili		+				
Liza macrolepis		+				
Valamugil cunnesius			+			
Drepane punctata			+			
Hilsa kelee			+			
Liza tricuspidens			+			
Mugil cephalus			+			
Otolithes ruber			+			Possibly over Continental Shelf
Pomadasys commersonni			+			
Rhabdosargus holubi			+			
Rhabdosargus sarba			+			Possibly in shallow water on 'shelf'
Johnius bellengerii			+	+		
Pomadasys hasta				+		Possibly inshore
Argyrosomus hololepidotus					+	
Elops machnata					+	
Gerres oyena					+	
Gerres punctatus					+	
Hypacanthus amia					+	
Lutianus argentimaculatus					+	
Muraenesox cinereus					+	
Megalops cyprinoides					+	
Platycephalus indicus					+	
Pomadasys multimaculatum					+	
Scomberoides commersonianus					+	
Therapon jarbua					+	
Tylosurus leirius					+	
Valamugil buchanani					+	

Table 11. Synoptic presentation of data obtained on areas of spawning (continued overleaf).

Species	In estuaries	In vicinity of estuary mouths	In marine inshore environment	In shallow water on continental shelf	In marine environment (details unknown)	Comments
Ambassis safga	+					
Gilchristella aestuarius	+					
Hyporhamphus knysnaensis	+					
Solea bleekeri	+					
Thryssa vitrirostris	+					
Species of Gobiidae	+					Plankton catches cast doubt on whether viable young are produced.

Table 11. Synoptic presentation of data obtained on areas of spawning.

SPECIES	RELATIVE ABUNDANCE A	VC	C	R	COMMENTS
Acanthopagrus berda	+				Riverbream, estuarine angling fish
Ambassis commersonni				+	Glassies, small estuarine species, food for predatory fish.
Ambassis gymnocephalus				+	
Ambassis natalensis	+				
Ambassis productus			+		
Argyrosomus hololepidotus		+			Kob, estuarine and marine, angling and commercial species.
Arothron immaculatus			+		Blaasop, small species, mainly marine.
Caranx ignobilis				+	Kingfish, marine angling fish.
Caranx sexfasciatus				+	
Chelondon patoca				+	Blaasop, small species, mainly marine
Chanos chanos				+	Milkfish, of value for human food and aquaculture
Crenidens crenidens				+	Karanteen, marine species, food for predatory fish, used for bait.
Diplodus sargus				+	Blacktail, marine inshore angling fish.
Drepane punctata				+	Concertina fish, marine inshore angling fish.
Elochelon luciae				+	Rare mullet.
Elops machnata	? See Text				Springer, estuarine and marine angling species.
Epinephelus andersoni				+	Rockcods, marine angling and commercial species.
Epinephelus tauvina				+	
Gaterin niger				+	Marine angling species.
Gerres acinaces				+	Pursemouths, estuarine and shallow marine species, non angling, valuable as human food.
Gerres oyena				+	
Gerres punctatus				+	
Gilchristella aestuarius	+				Small estuarine species, food for predatory fish.
Gobiidae			+		Gobies, small species, food for predatory fish.
Hilsa kelee				+	Kelee shad, commercial shallow water species, valuable as human food.
Hypacanthus amia				+	Leervis, estuarine and marine angling species.
Hyporhamphus knysnaensis	+				Halfbeak, small species, food for predatory fish.
Johnius belengerii			+		Mini-kob, small species, not important for angling or human food.
Leiognathus equulus		+			Slimy, small species, not important for angling or human food.

Table 12. Relative abundance of juveniles of species which occur in Natal estuaries. Common names and comments on their 'usefulness to man' have been included to provide greater insight into the importance of estuaries in the biology of the fishes of Natal. A = abundant; VC = very common; C = common; R = rare. (Continued overleaf).

SPECIES	RELATIVE ABUNDANCE A	VC	C	R	COMMENTS
Liza alata				+	Mullet, valuable as human food.
Liza dumerili	+				Mullet, valuable as human food.
Liza macrolepis	+				Mullet, valuable as human food.
Liza tricuspidens				+	Mullet, valuable as human food.
Lutjanus argentimaculatus				+	River snapper, mainly marine angling species.
Lutjanus fulviflamma			+		Dory snapper, small species, not important for angling or human food
Monodactylus sp.			+		Small species, not important for angling or human food.
Mugil cephalus	+				Mullet, valuable for human food and aquaculture.
Myxus capensis			+		Mullet, valuable as human food.
Pelates quadrilineatus			+		Small species, not important for angling or human food.
Platycephalus indicus				+	Flathead, estuarine and marine angling fish.
Pomadasys commersonni	+				Spotted grunter, estuarine and marine angling fish.
Pomadasys hasta			+		Javelin grunter, mainly marine angling species.
Pomatomus saltatrix				+	Elf, marine angling species.
Rhabdosargus holubi	+				Cape stumpnose, mainly marine angling species.
Rhabdosargus sarba	+				Natal stumpnose, estuarine and marine angling species.
Sauvagella madagascariensis			+		Small estuarine species, food for predatory fish.
Siganus sp.				+	Rabbitfish, mainly marine.
Solea bleekeri		+			Sole, small species, food for predatory fish.
Sphyraena sp.				+	Barracuda, marine angling fish.
Stolephorus commersonni		+			Anchovy, small species, food for predatory fish.
Therapon jarbua			+		Thornfish, small species of little value for angling or human food.
Thryssa vitrirostris			+		Glassnose, small species, food for predatory fish, used for bait.
Valamugil buchanani		+			Mullet, valuable as human food.
Valamugil cunnesius		+			Mullet, valuable as human food.

Table 12. (Continued).
A = abundant; VC = very common; C = common; R = rare.

Species	Length Class (cm)	NATAL									TRANSKEI					CAPE EAST AND SOUTH COASTS									CAPE WEST COAST
		Kosi Lakes	St. Lucia Lakes	Richards Bay	Amatikulu R.	Zinkwazi R.	Umhlanga R.	Durban Bay	Umgababa R.	Southbroom R.	Msikaba R.	Ntafufu R.	Ntakatye R.	Xora R.	Qora R.	Kwelera R.	Keiskamma R.	Kleinemond R.	Swartkops R.	Kromme R.	Keurbooms R.	Knysna Lagoon	Breede R.	Klein R.	Berg R.
Acanthopagrus berda	0–3		+	+	+																				
	3–6		+	+	+		+				+														
	6–9		+	+	+		+																		
	9–12		+	+	+																				
Argyrosomus hololepidotus	0–3																								
	3–6		+																						
	6–9		+	+													+								
	9–12		+	+													+								
Liza dumerili	0–3		+	+						+	+	+	+	+	+				+						
	3–6		+	+	+		+	+		+	+	+	+	+	+		+		+	+			+		
	6–9		+	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+		+		
	9–12		+	+	+	+		+		+	+	+	+	+	+	+	+		+	+			+		
Liza macrolepis	0–3	+	+	+	+		+				+	+	+	+											
	3–6	+	+	+	+						+		+	+						+					
	6–9	+	+	+				+		+	+		+	+			+				+				
	9–12	+	+	+				+			+			+			+								
Mugil cephalus	0–3	+	+	+	+	+			+		+		+			+			+	+			+		
	3–6	+	+	+	+		+	+	+	+	+						+			+			+		
	6–9		+	+	+					+	+									+		+			
	9–12		+	+	+	+		+									+			+					

Table 13. Distribution of juveniles of the main species of estuarine fish of Natal along the coast of South Africa. (Continued overleaf).

Species	Length Class (cm)	NATAL									TRANSKEI					CAPE EAST AND SOUTH COASTS									CAPE WEST COAST
		Kosi Lakes	St. Lucia Lakes	Richards Bay	Amatikulu R.	Zinkwazi R.	Umhlanga R.	Durban Bay	Umgababa R.	Southbroom R.	Msikaba R.	Ntafufu R.	Ntakatye R.	Xora R.	Qora R.	Kwelera R.	Keiskamma R.	Kleinemond R.	Swartkops R.	Kromme R.	Keurbooms R.	Knysna Lagoon	Breede R.	Klein R.	Berg R.
Pomadasys commersonni	0–3		+																						
	3–6		+	+	+			+				+													
	6–9		+	+	+		+	+	+			+		+	+		+	+							
	9–12		+	+	+			+			+	+			+		+								
Rhabdosargus holubi	0–3		+	+	+			+			+	+	+	+	+	+	+	+	+	+	+			+	
	3–6		+	+	+		+	+		+	+	+	+	+	+	+	+		+		+	+		+	
	6–9		+	+	+			+			+	+	+	+	+	+	+		+	+		+		+	
	9–12		+	+	+			+			+	+	+	+	+	+	+		+	+		+	+	+	
Rhabdosargus sarba	0–3		+	+				+																	
	3–6		+	+	+			+			+	+	+												
	6–9		+	+								+	+												
	9–12		+	+				+			+		+												
Valamugil buchanani	0–3		+	+																					
	3–6		+	+	+			+		+	+		+	+											
	6–9		+	+	+			+			+	+	+	+											
	9–12		+	+	+			+			+		+												
Valamugil cunnesius	0–3		+	+																					
	3–6		+	+	+		+	+																	
	6–9		+	+	+		+	+																	
	9–12		+	+	+			+																	

Table 13. Distribution of juveniles of the main species of estuarine fish of Natal along the coast of South Africa.

Species	NATAL									TRANSKEI					CAPE EAST AND SOUTH COASTS									CAPE WEST COAST
	Kosi Lakes	St. Lucia Lakes	Richards Bay	Amatikulu R.	Zinkwazi R.	Umhlanga R.	Durban Bay	Umgababa R.	Southbroom R.	Msikaba R.	Ntafufu R.	Ntakatye R.	Xora R.	Qora R.	Kwelera R.	Keiskamma R.	Kleinemond R.	Swartkops R.	Kromme R.	Keurbooms R.	Knysna Lagoon	Breede R.	Klein R.	Berg R.
Gerres acinaces	+	+									+													
Gerres oyena	+	+	+				+				+													
Gerres punctata	+	+	+	+			+				+													
Hypacanthus amia		+	+					+			+	+			+	+	+	+	+					
Lithognathus lithognathus																+	+	+		+	+		+	
Liza richardsoni															+	+		+	+	+	+	+	+	+
Liza tricuspidens		+								+	+	+	+	+	+	+		+	+		+	+		
Myxus capensis		+	+		+				+	+	+	+		+							+			
Pomadasys hasta		+	+	+		+																		
Rhabdosargus globiceps																			+		+	+	+	
Therapon jarbua		+	+	+	+	+			+	+	+	+	+											

Table 14. Distribution of juveniles of estuarine fish species along the coast of South Africa (data for the main estuarine species of Natal are given in Table 13).

Netting Gear	Period	Number of Fish	Change in mean length (mm)	Slope of regression (= daily growth increment mm)	Monthly growth increment (mm)
Drag net	Sept. to Dec. 1969	455	61.2 - 102.3	0.4832	14.7
Shrimp trawl	Dec. 1969 to April 1970	240	91.7 - 138.6	0.3942	12.0
	Jan. to April 1971	386	82.1 - 118.4	0.3958	12.0

Table 15. Estimates of the monthly growth increments of juvenile grunter (*Pomadasys commersonni*) based on the mean lengths of catches made in different types of netting gear.

	LENGTH CLASSES (cm)																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
J																				
F															2	1	3	1	3	
M									1		1		3	2		1				
A									2		3	3	1		2	2				
M																				
J									7	4	9	6	2	1	1	3				
Jl																				
A									1	3	2	1								
S									6		2									
O																				
N																				
D													1	3	20	7	4	1		

Table 16. Length composition of catches of juvenile *Elops machnata* in Natal estuaries (1969-1971; N=115).

	LENGTH CLASSES (cm)																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
J																				
F																				
M																				
A						1														
M						1														
J																				
Jl																				
A		6																		
S		13																		
O		8	9																	
N		19	16	3																
D		1	3																	

Table 17. Length composition of catches of juvenile *Myxus capensis* in Natal estuaries (1969-1971; N=80).

	LENGTH CLASSES (cm)																				
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
J								1	2											1	
F								2	7	9	1	2									
M					6	1	4	4	2	1	1	2	1								
A					1				2	2	2	1			1	1	1		1		
M								5	13	20	17	7	5		2	1					
J							1	12	8	14	3	5	1	2							
Jl								3	8	12	9	7	2	1							
A					1			2	6	5	4	5		1	2						
S								3	7	12	12	8	1	2	1						
O							1		5	3	5	4	5	4	3						
N					1			2	7	6	2	1	1		3	1					
D										1		2									

Table 18. Length composition of catches of juvenile Pomadasys hasta in Natal estuaries (1969-1971; N=346)

	LENGTH CLASSES (cm)																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
J	2		2	3	2	2		2											
F	1	1	1				1					3	2	2	1	2			
M	1							1	1										
A	3	2	5	7	3	4	2	1	3			1	1	1					
M	7	4	1	12	12	1	4	17	12	9	3	2	3	1		1			
J			1	14	14	17	14	9	10	3									
Jl			8	15	16	12	21	7	5	2	1								
A					1	5	5		1	1	2								
S			7	12	2	3		5	2	1	1								
O			1	2				3	2										
N	16		1				2	4	2	4	1								
D	3		1			3	2	1	1		1	1				1			

Table 19. Length composition of catches of juvenile Therapon jarbua in Natal estuaries (1969-1971; N=410).

	LENGTH CLASSES (cm)																				
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
J			8		2	6	5	1													
F																					
M			1																		
A			2	4																	
M		1	3	2	9																
J			2					1													
Jl																					
A						8	1				2	2									
S				3	1	1					1	2	5								
O		1	4																		
N														3	3	1	2	1	1		
D		1							2	8	7	2	1								

Table 20. Length composition of catches of juvenile *Thryssa vitrirostris* in Natal estuaries (1969-1971; N=110)

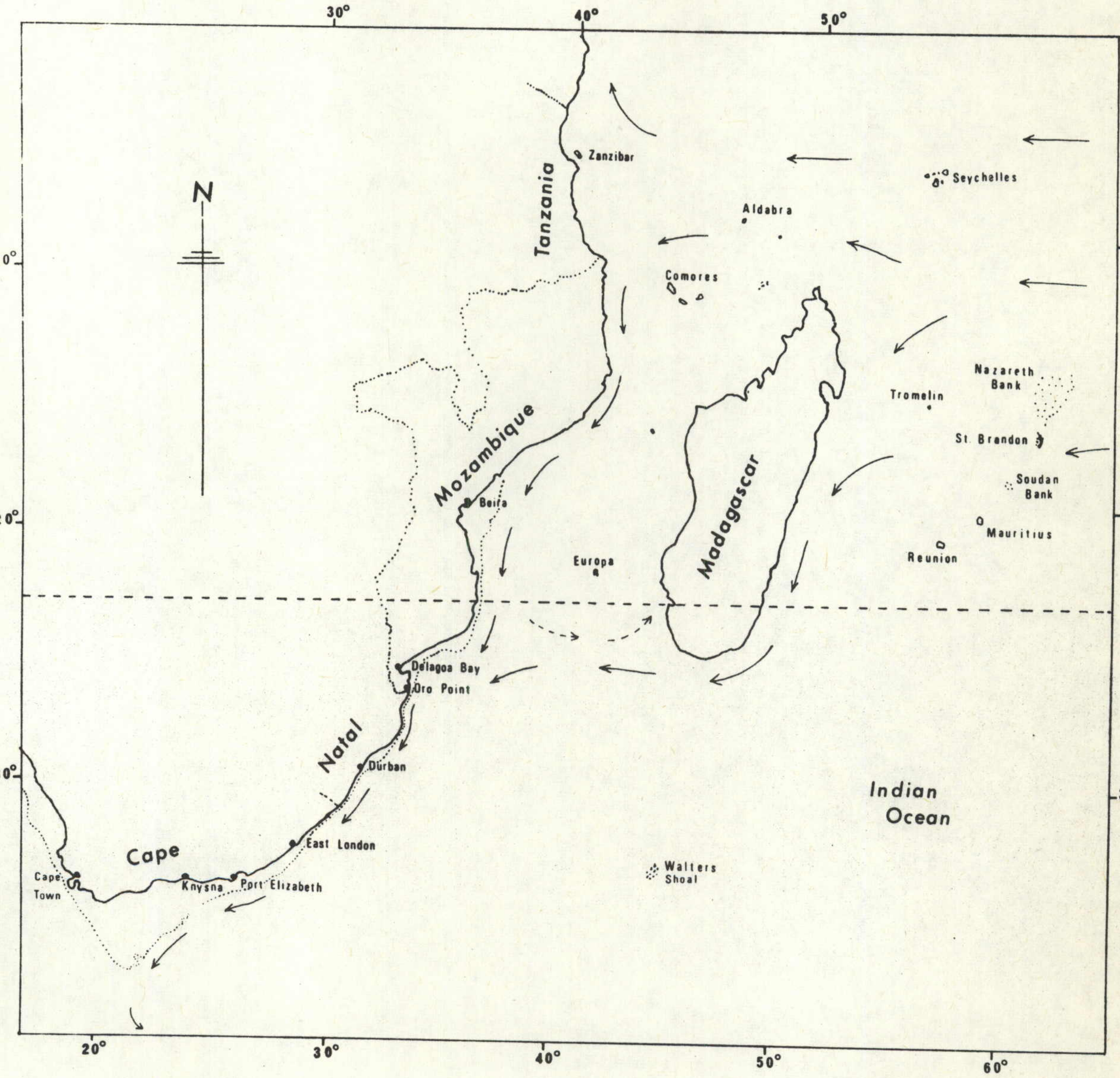


Figure 1. Major current systems of the south-west Indian Ocean. The 100 fathom depth contour is shown as a dotted line from Beira southwards along the African coast (after Bass *et al*, 1973).

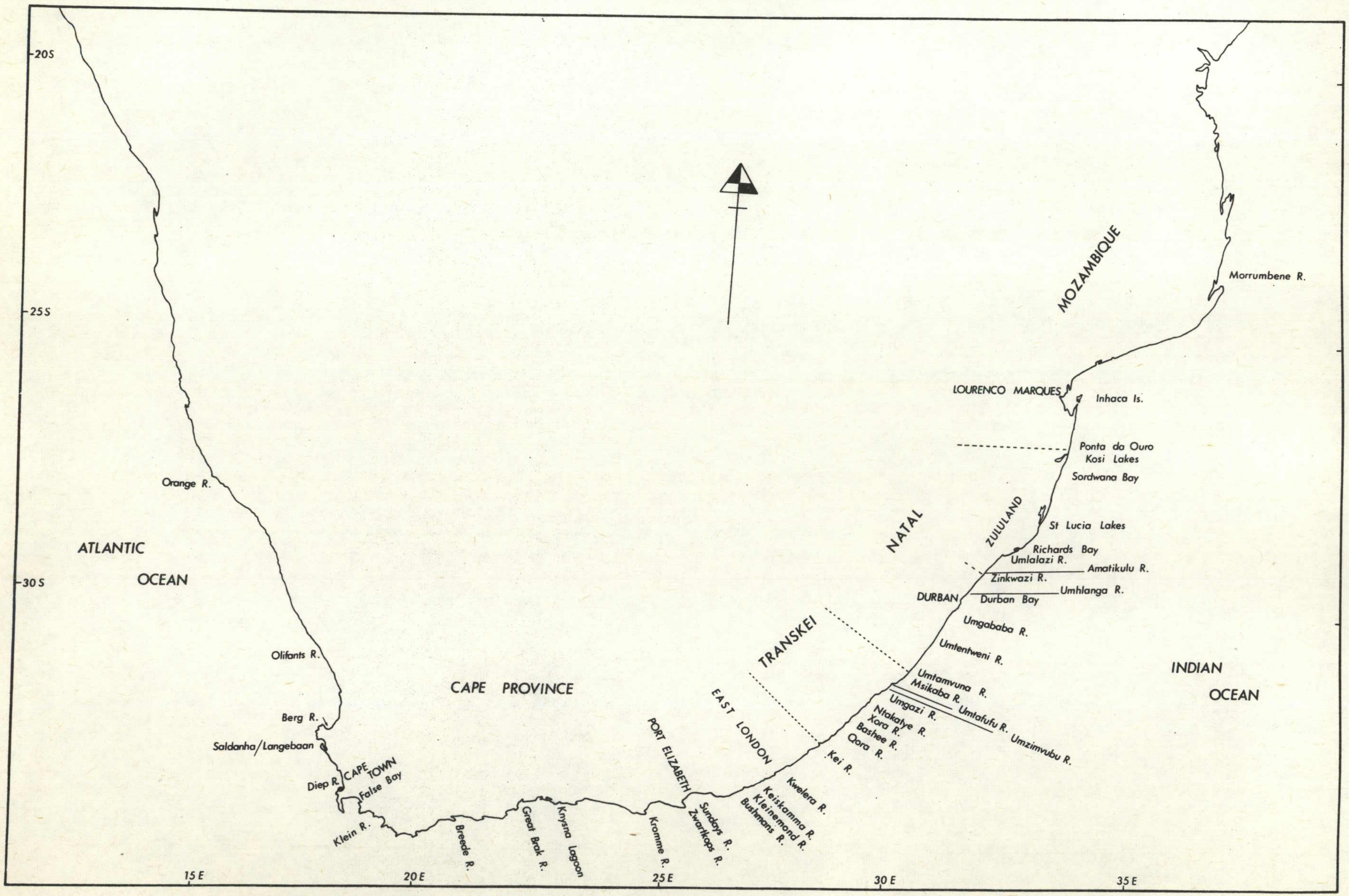


Figure 2. Map of Southern Africa showing the localities mentioned in the text.

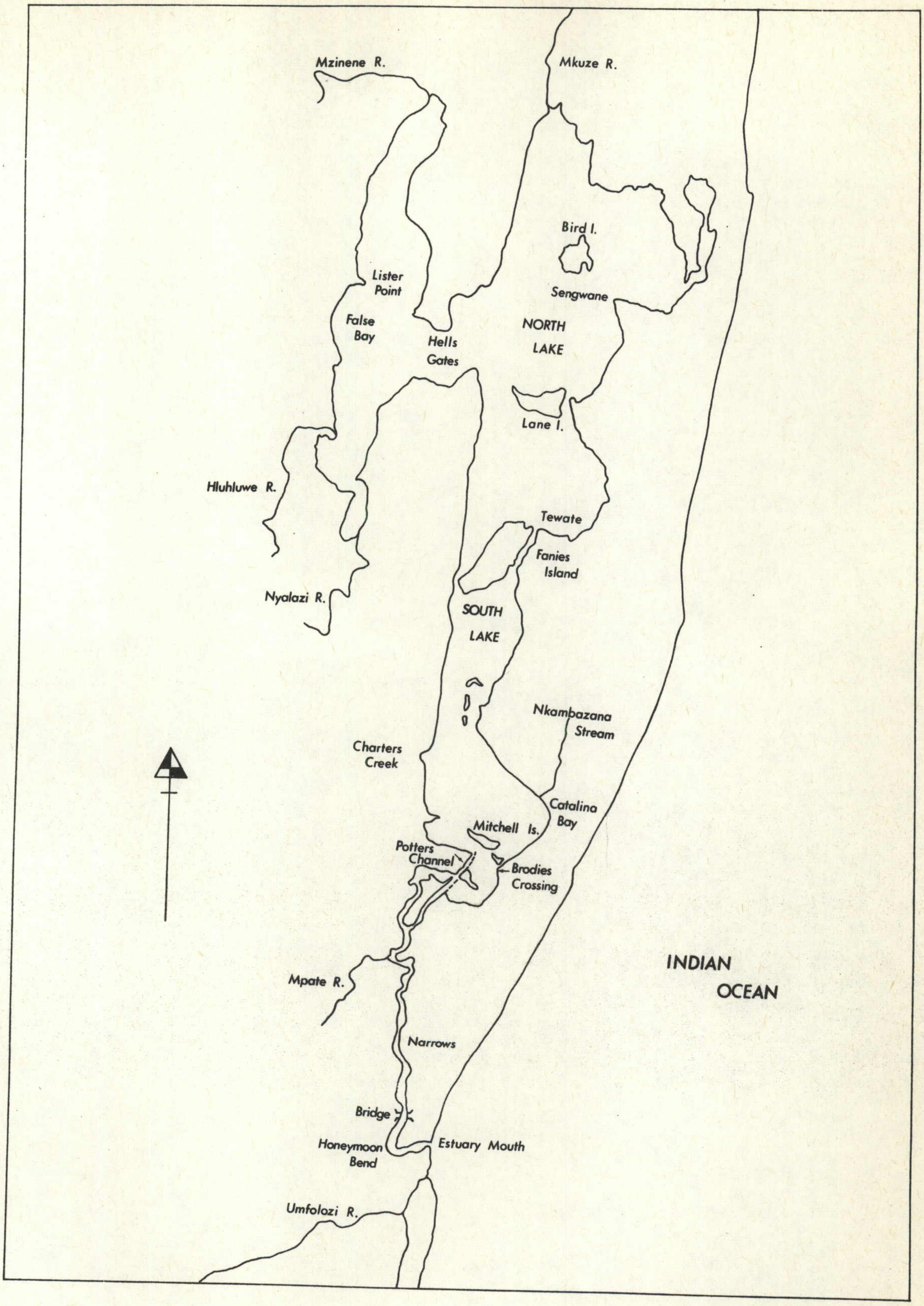


Figure 3. Map of the St. Lucia Lake System

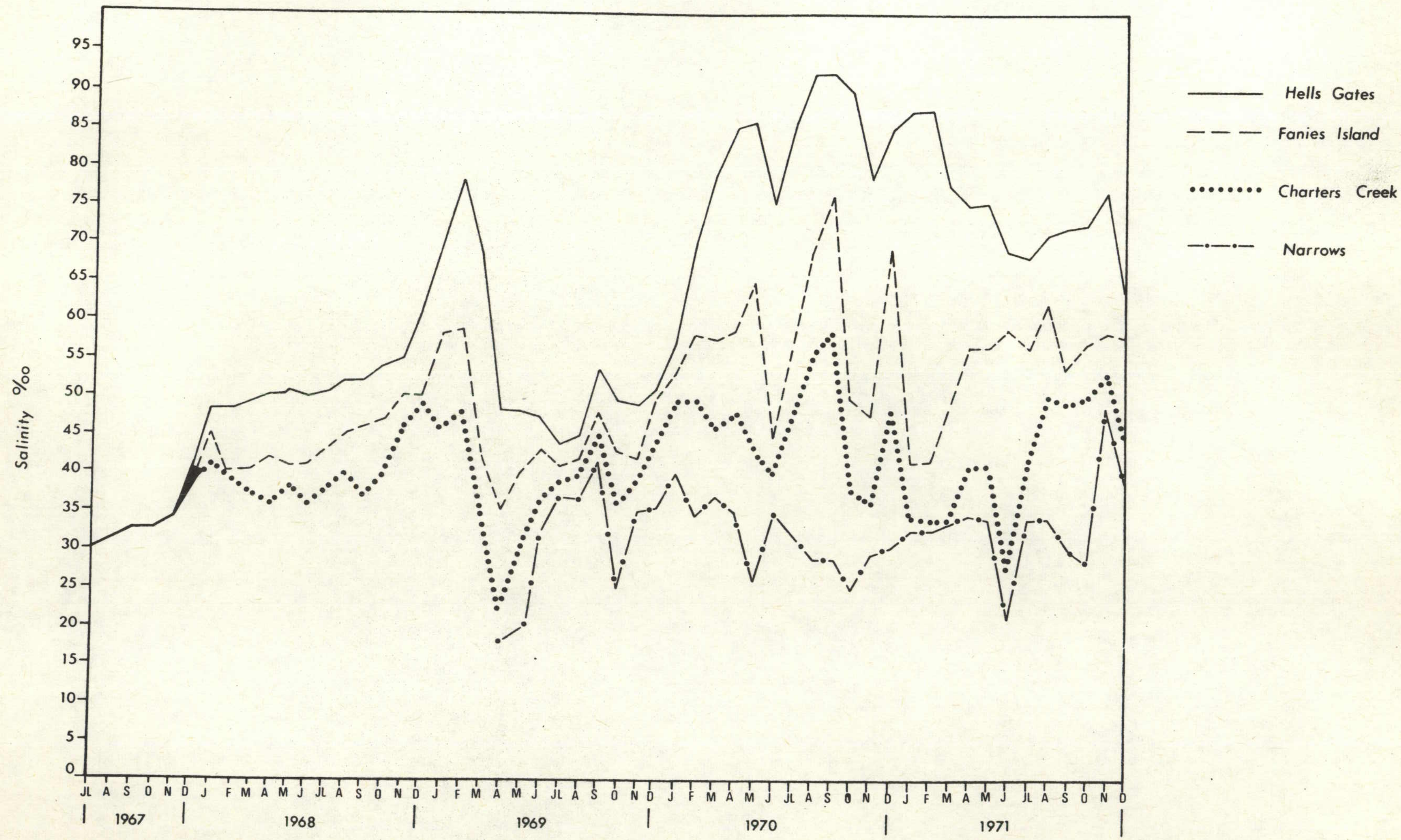


Figure 4. Salinity regime in the St. Lucia Lake System shortly before and during the research period. (The sampling stations are indicated in Figure 3.).

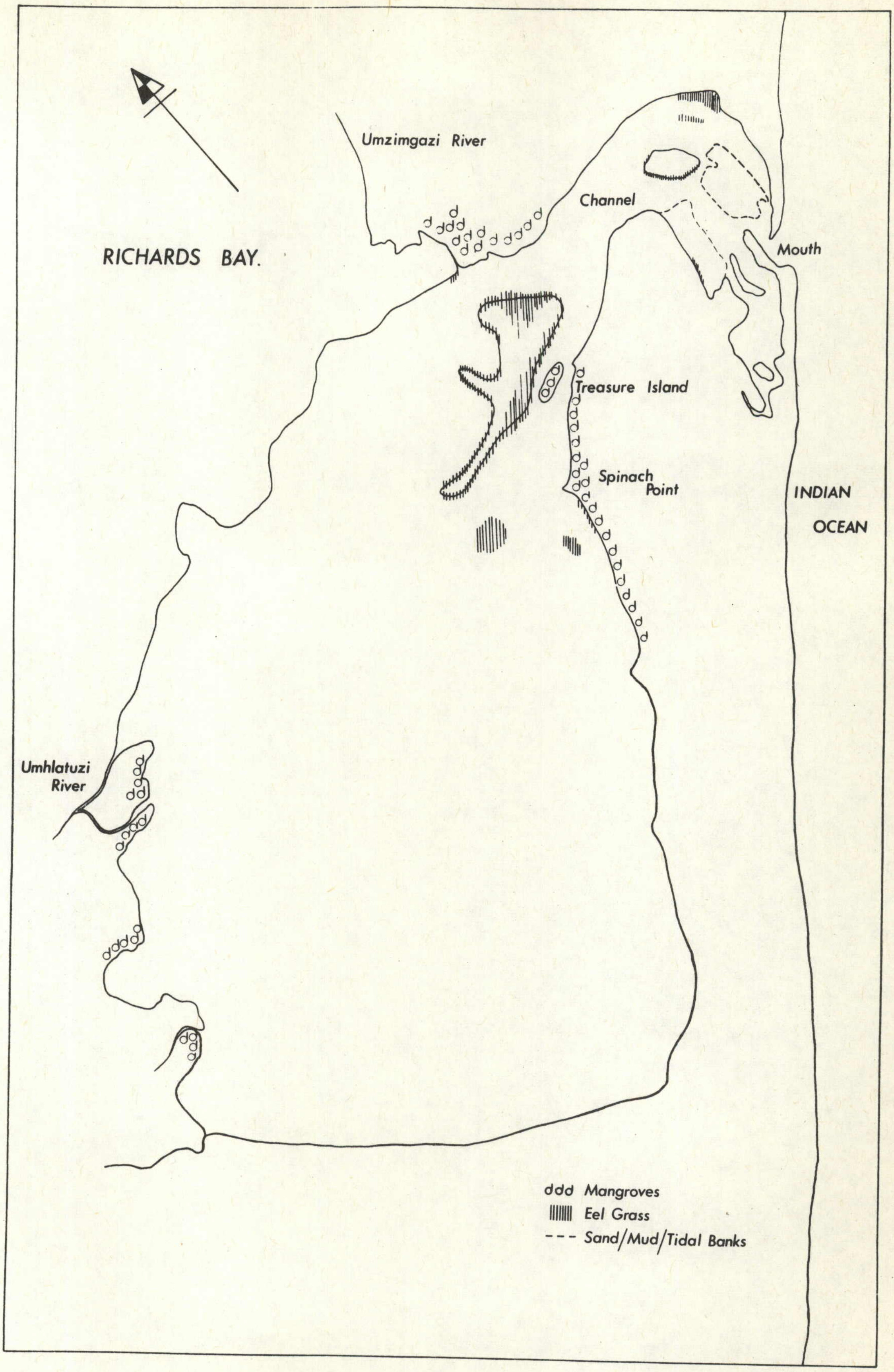


Figure 5. Map of Richards Bay.

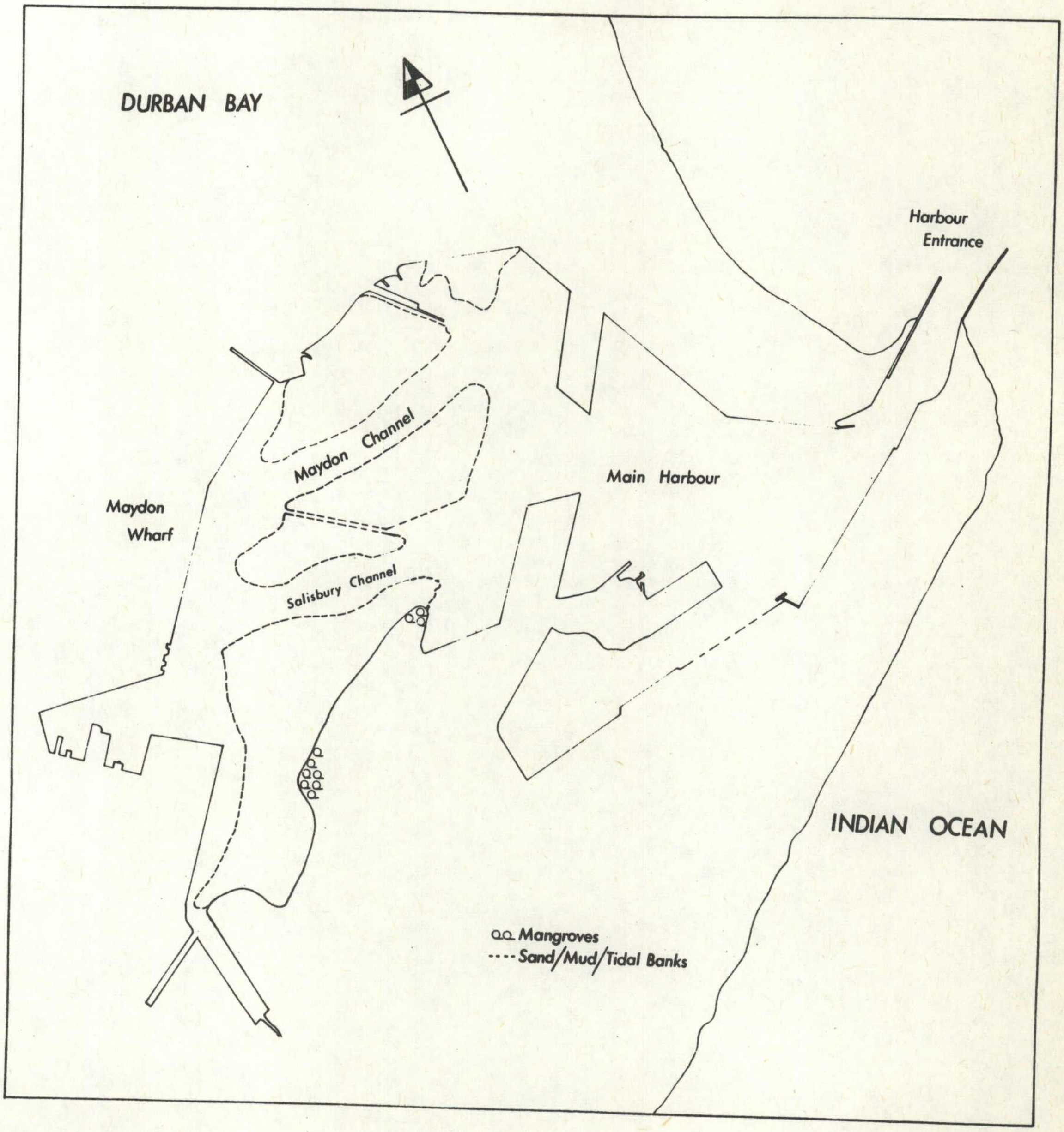


Figure 6. Map of Durban Bay

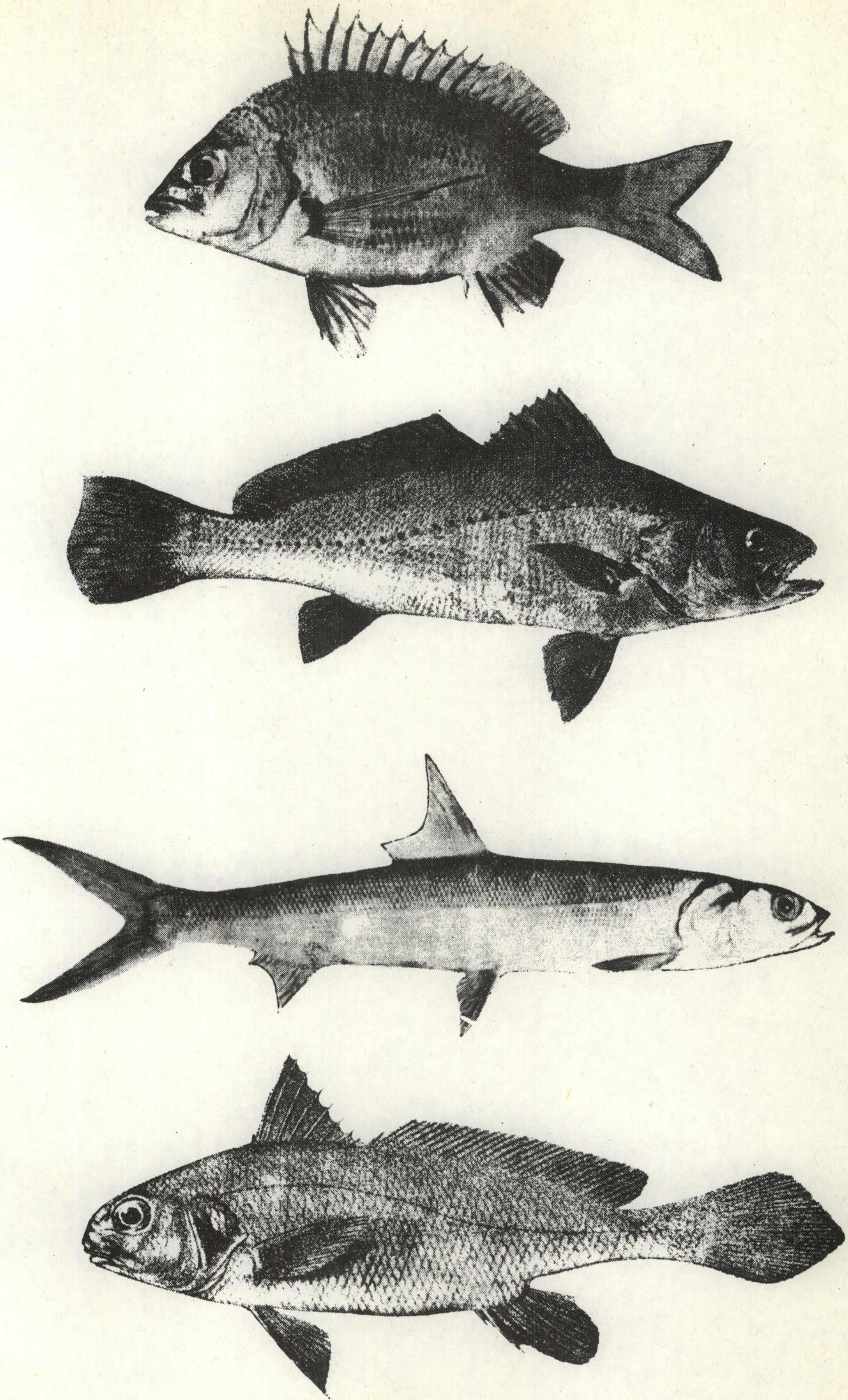


Figure 7. Important species mentioned in the text (after Smith, 1949) *Acanthopagrus berda*; *Argyrosomus hololepidotus*; *Elops machnata*; *Johnius belengerii*. (Continued overleaf).

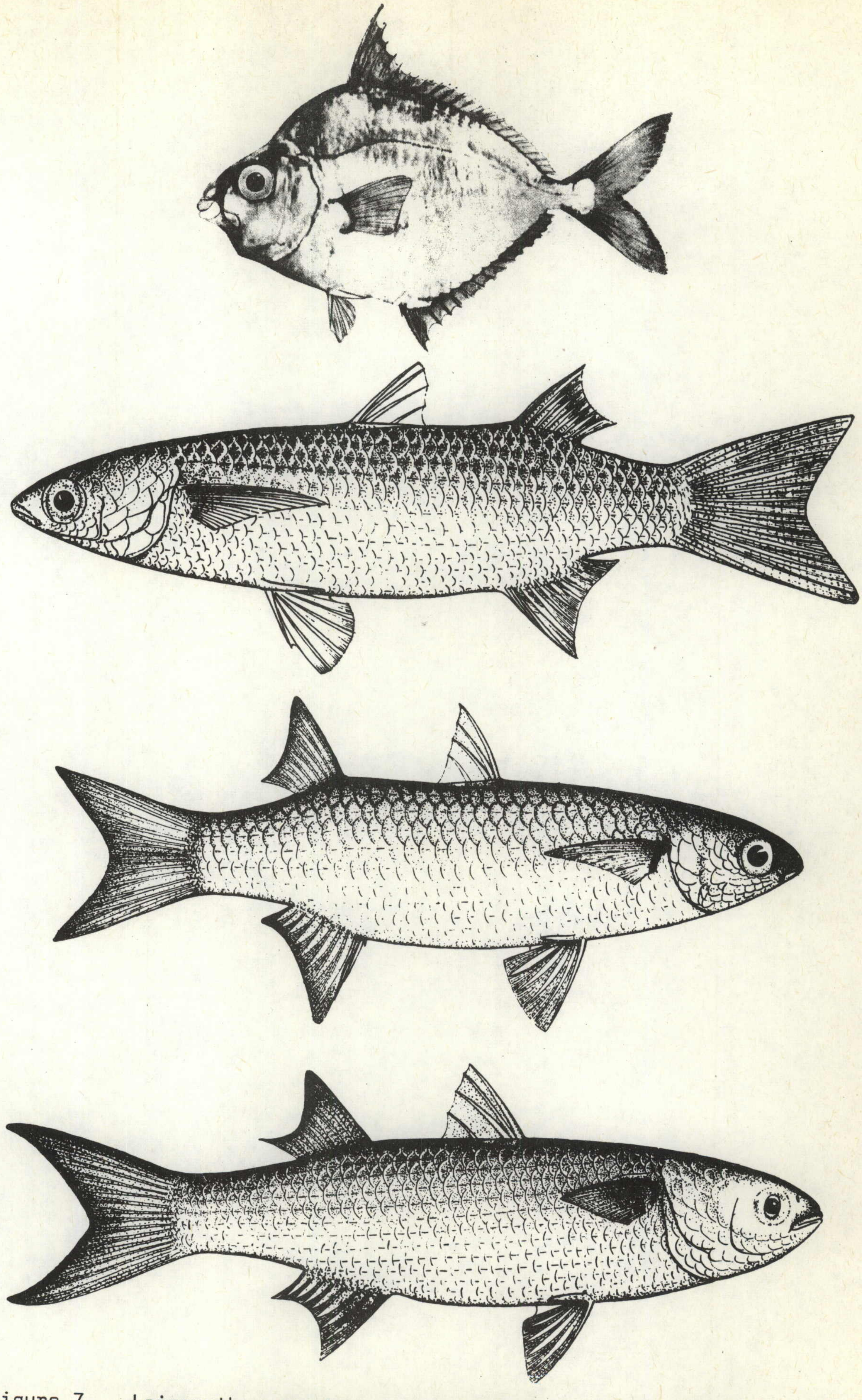


Figure 7. Leiognathus equulus; Liza dumerili; Liza macrolepis; Mugil cephalus. (Continued overleaf).

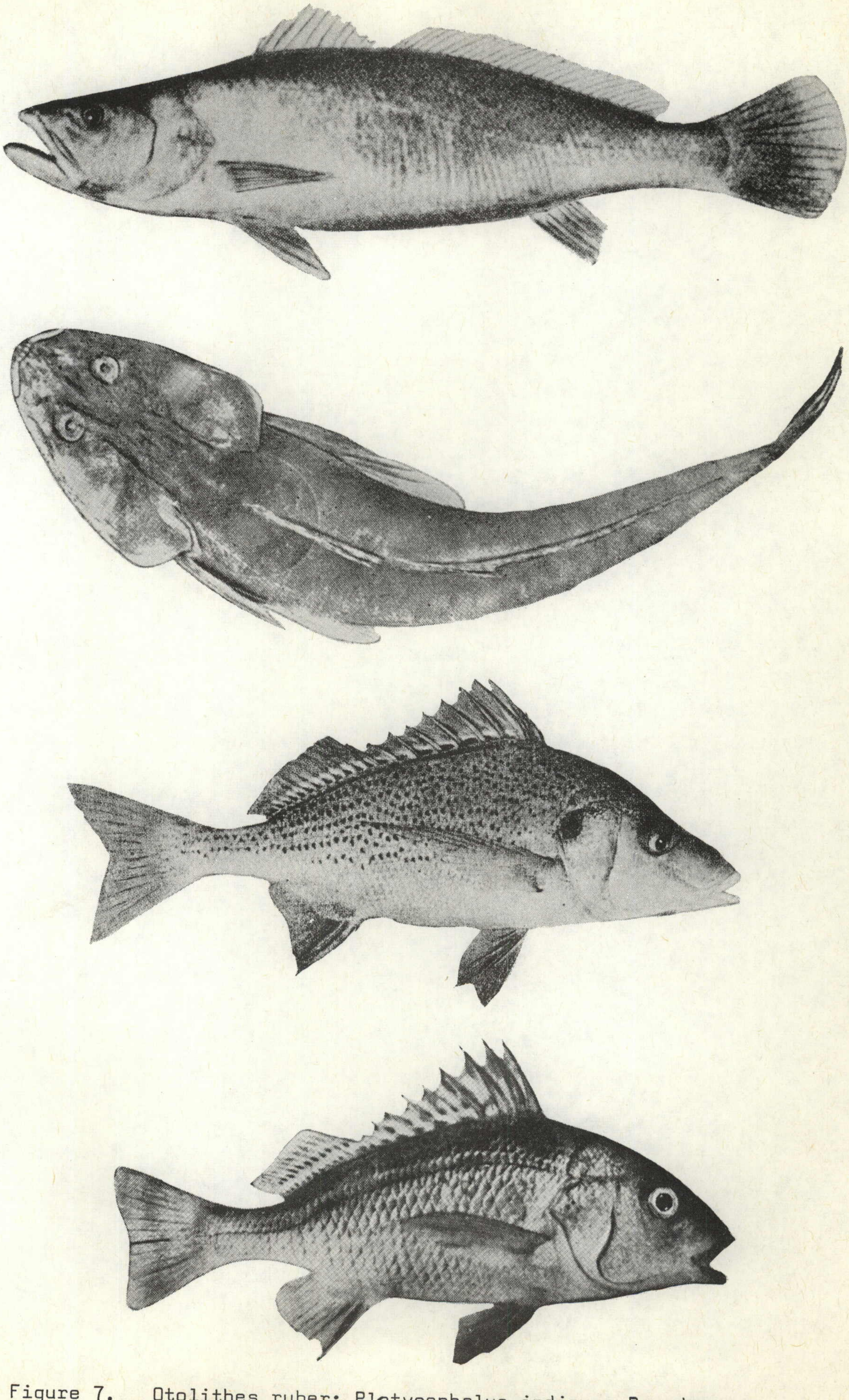


Figure 7. Otolithes ruber; Platycephalus indicus; Pomadasys commersonni; Pomadasys hasta. (Continued overleaf).

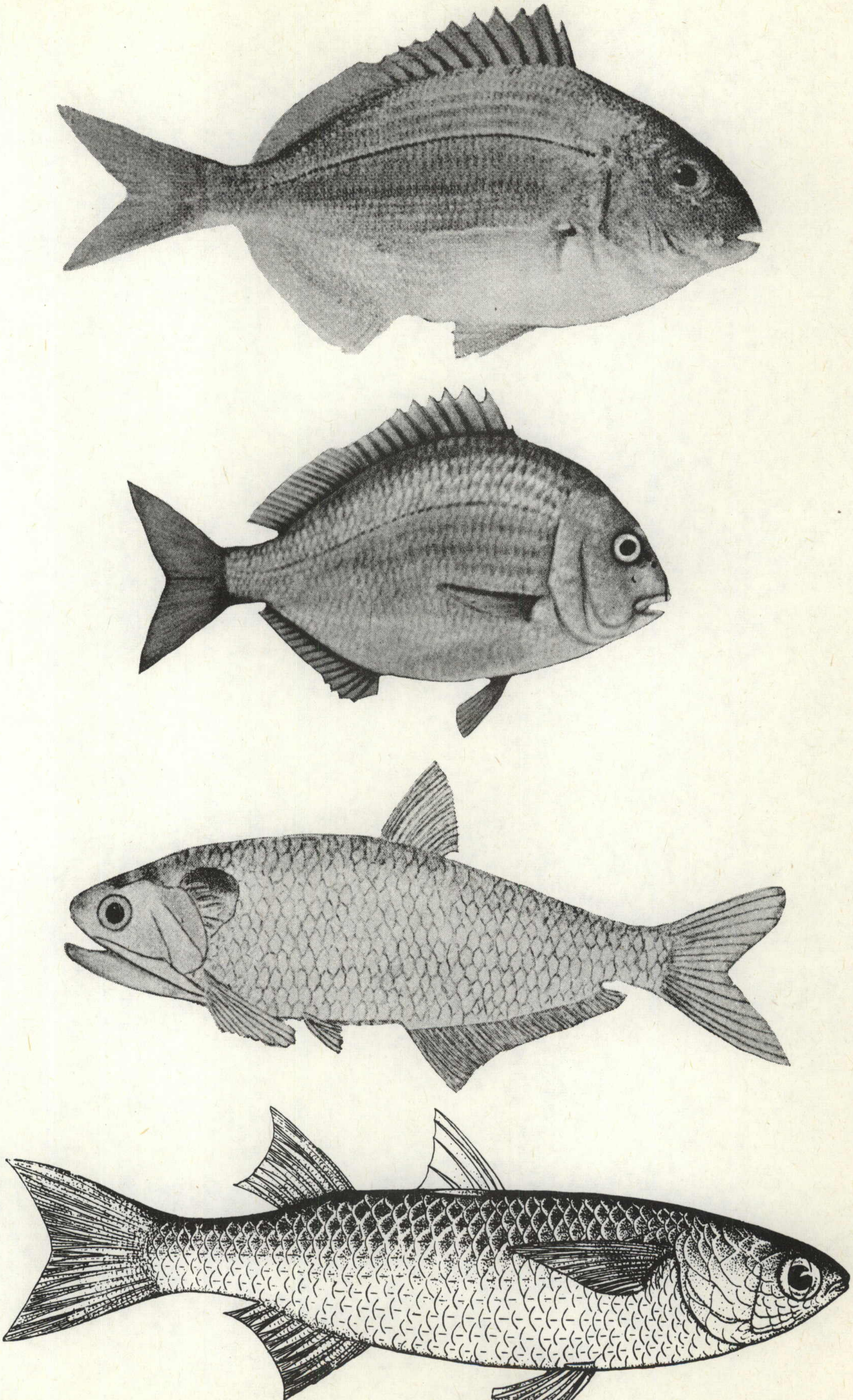


Figure 7. Rhabdosargus holubi; Rhabdosargus sarba; Thryssa vitrirostris; Valamugil cunnesius.

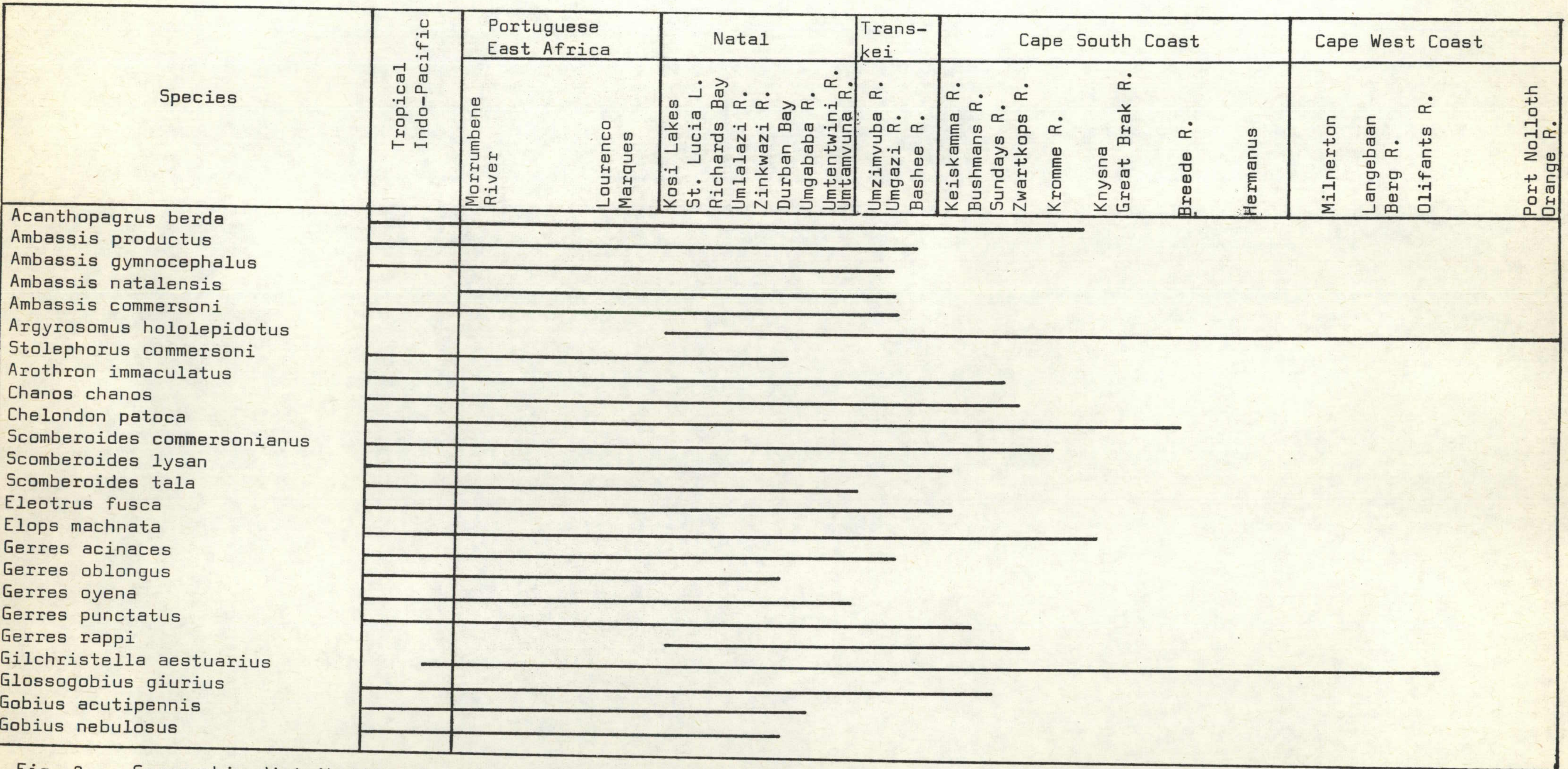


Fig. 8 Geographic distribution of common euryhaline fishes on the coast of southern Africa. (Continued overleaf). (Sources of information include the distributional records of the: Oceanographic Research Institute (Durban); Dept. of Zoology, University of Cape Town; J.L.B. Smith Institute of Ichthyology, Grahamstown).

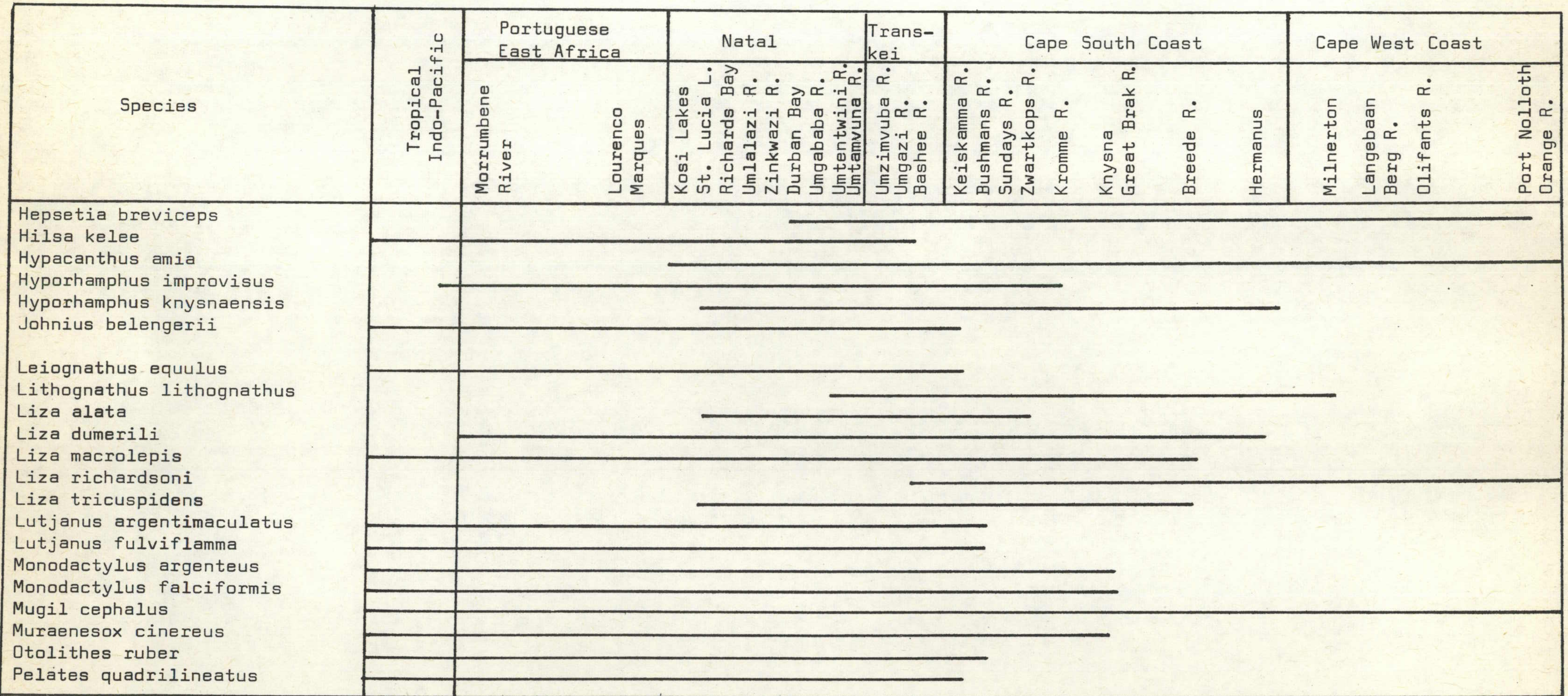


Fig. 8 (Continued)

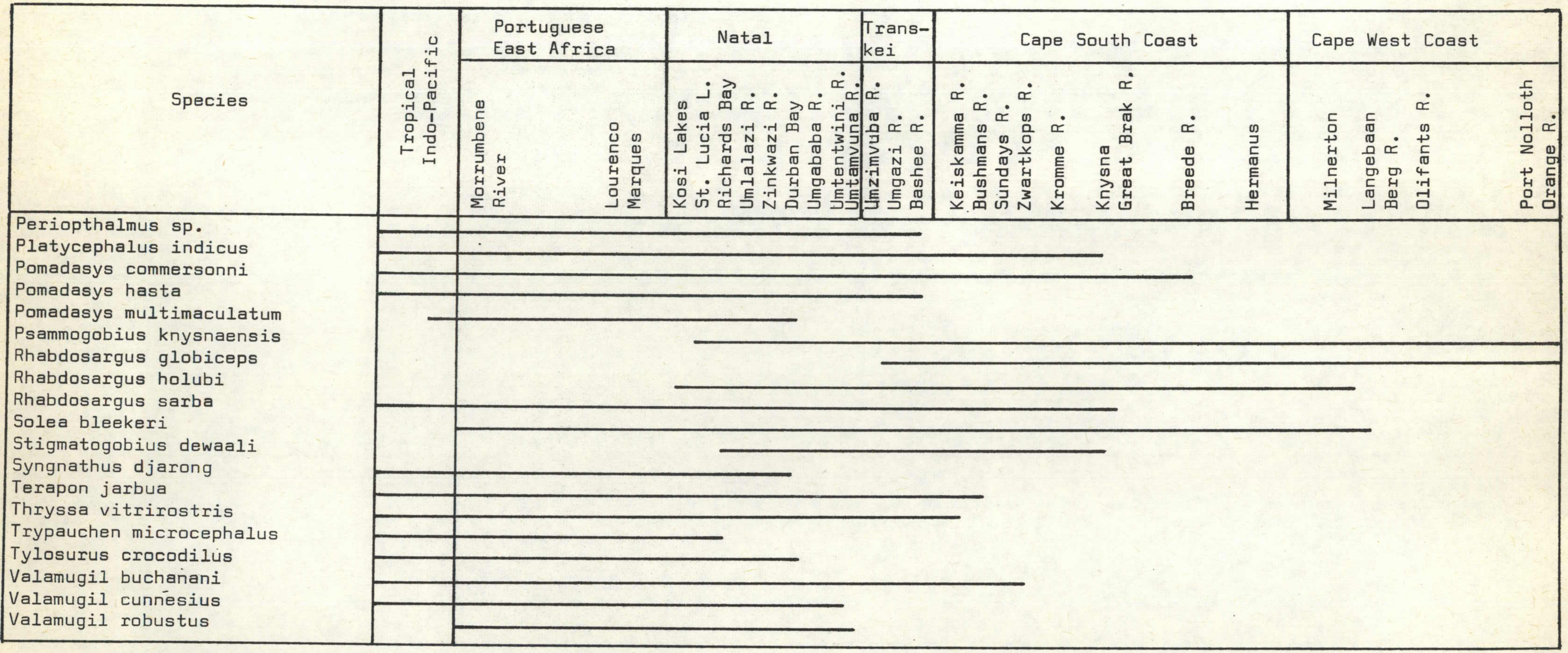


Fig. 8 (Continued).

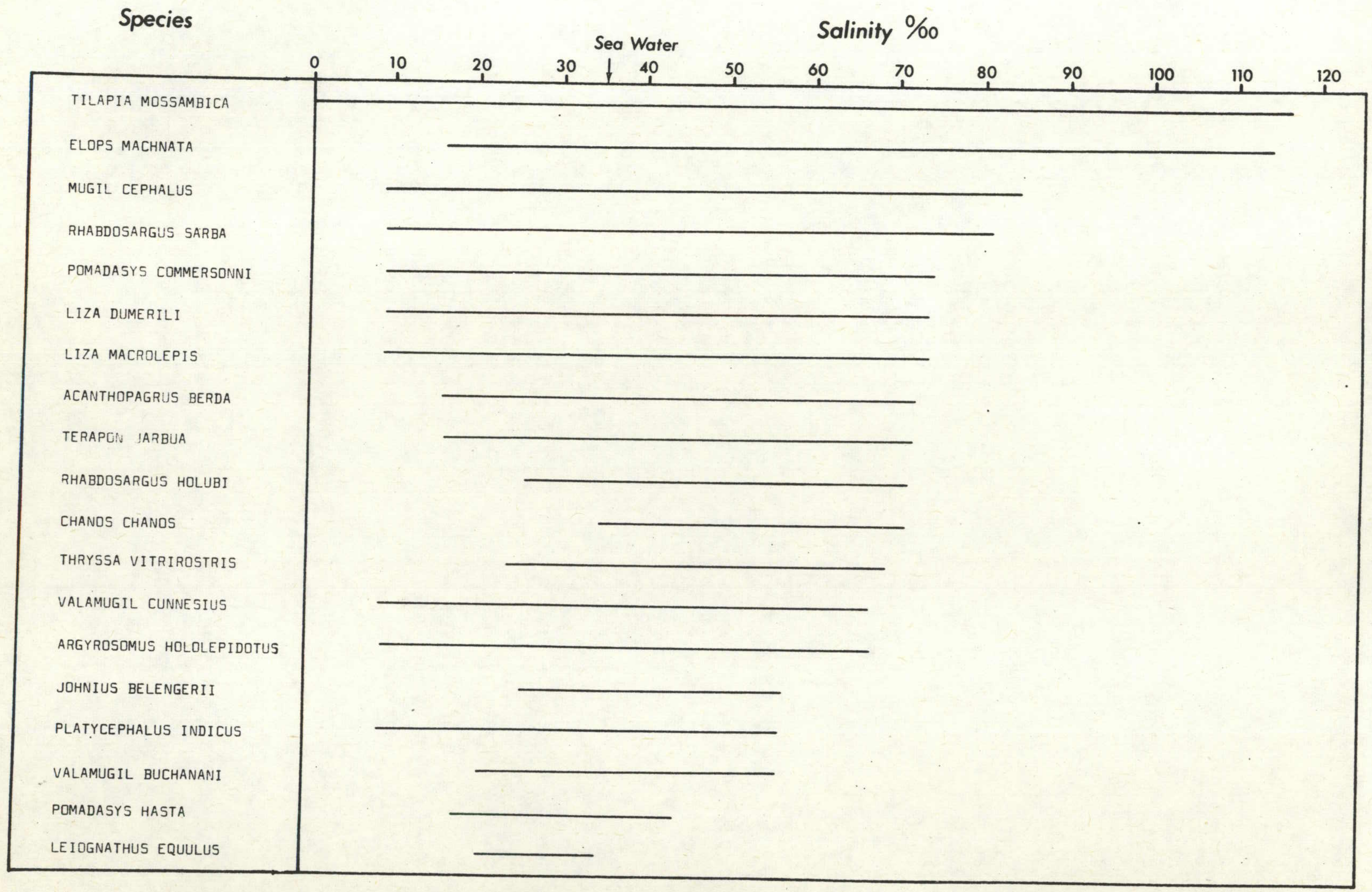


Figure 9. Ranges of salinity tolerance of species recorded in the St. Lucia lake system.

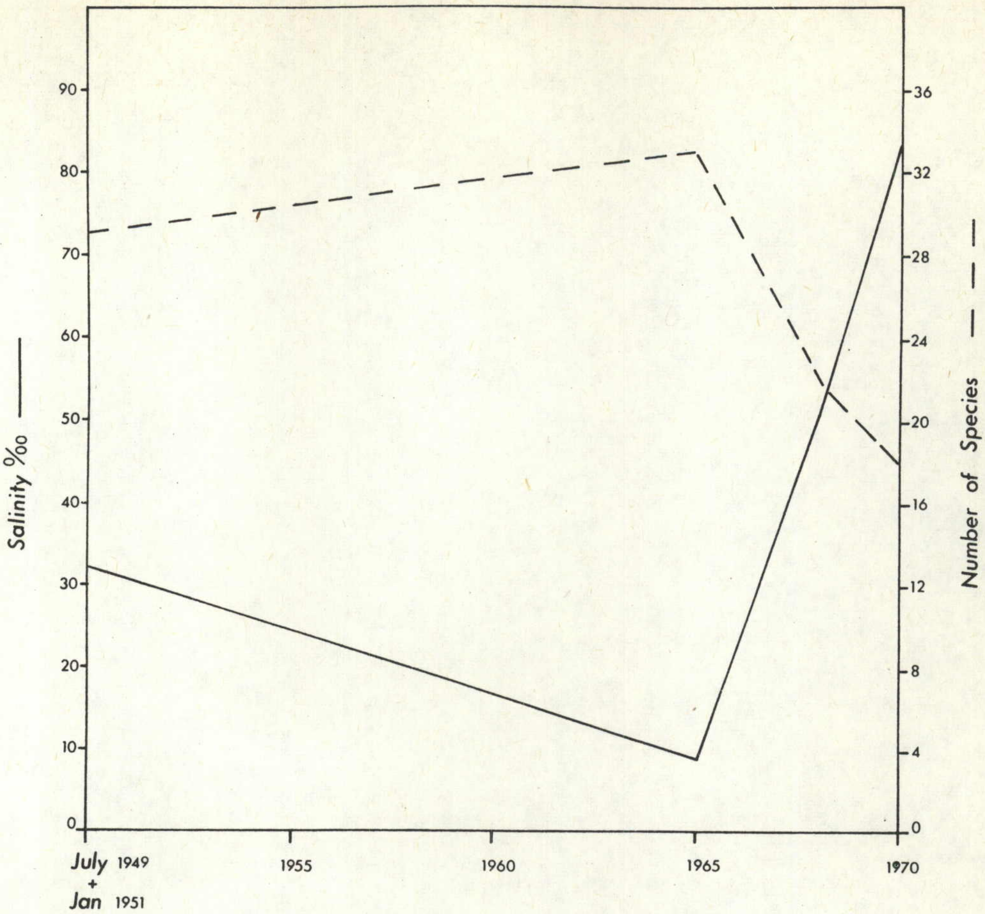


Figure 10. Relationship between the number of species of fish recorded north of Fanies Island and the salinity of the north lake (Hells Gates salinities plotted).

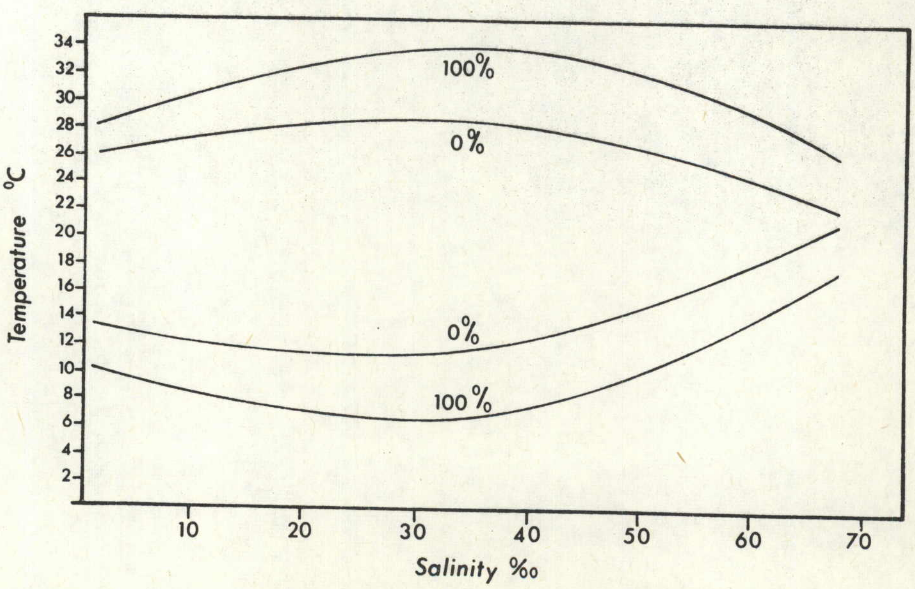


Figure 11. 0% and 100% mortality curves for juvenile <u>R. holubi</u> under 36 combinations of temperature

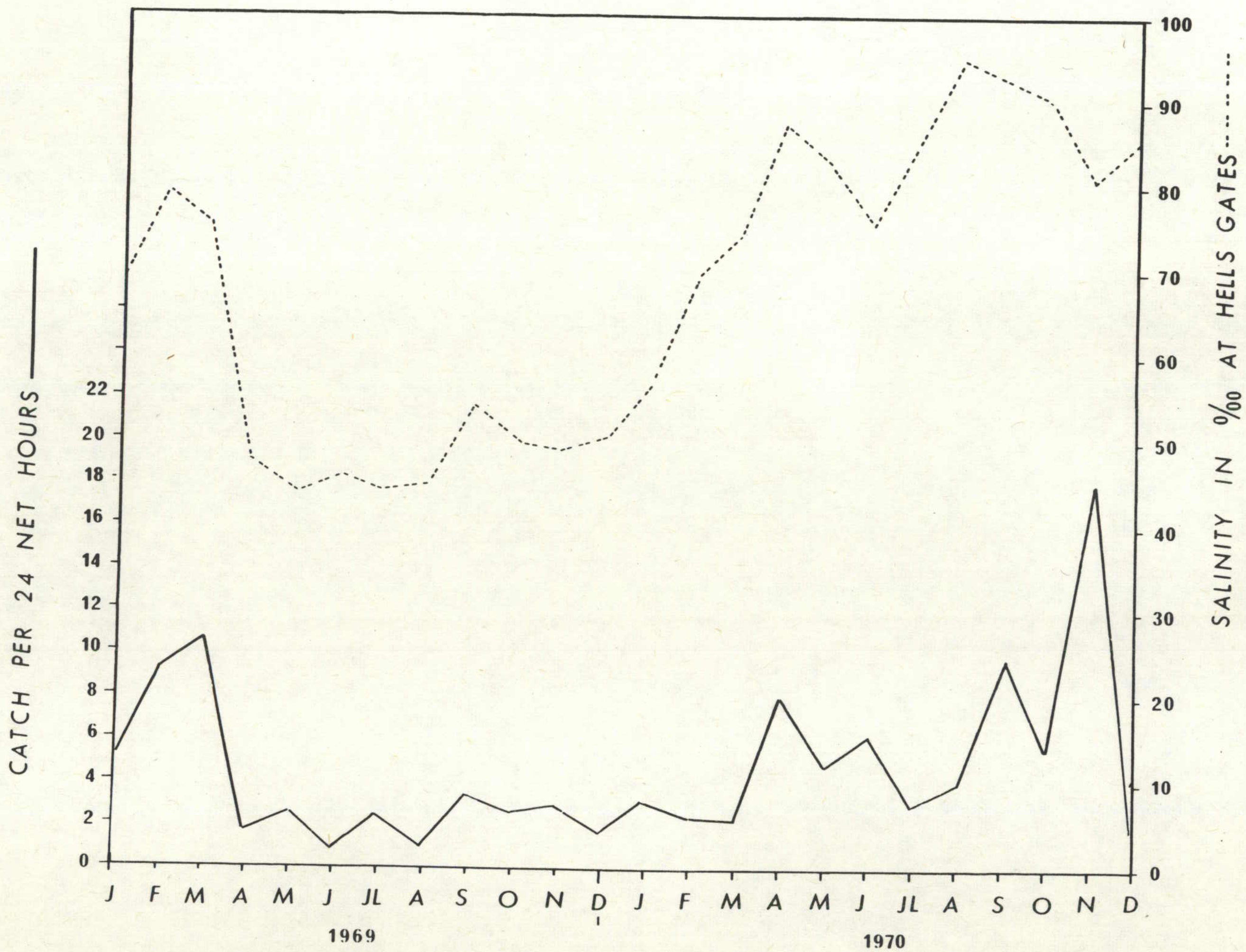


Figure 12. Relationship between salinity in St. Lucia north lake and the abundance of <u>Argyrosomus hololepidotus</u> in the south lake.

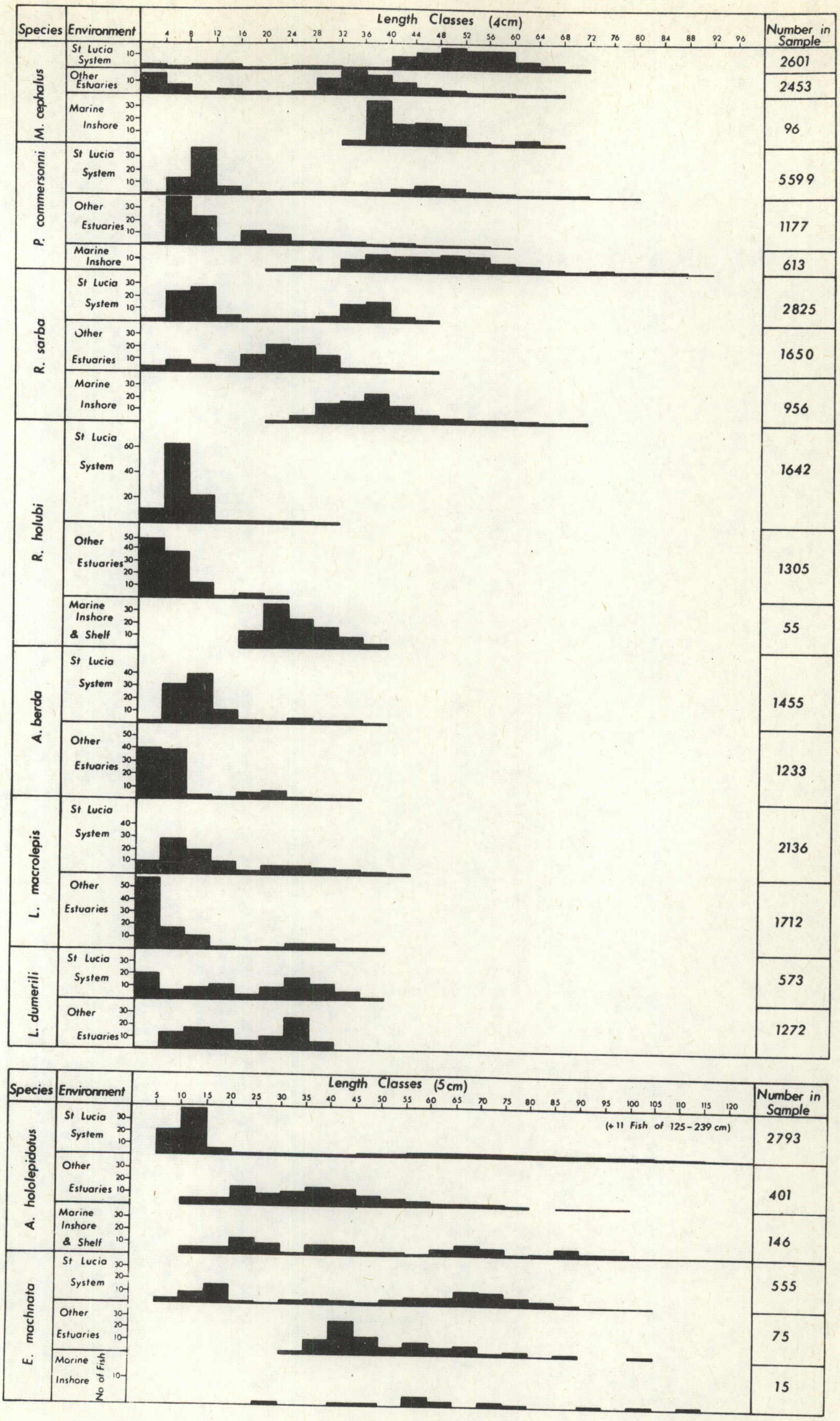


Figure 13. Percentage length composition of catches from different Natal environments.

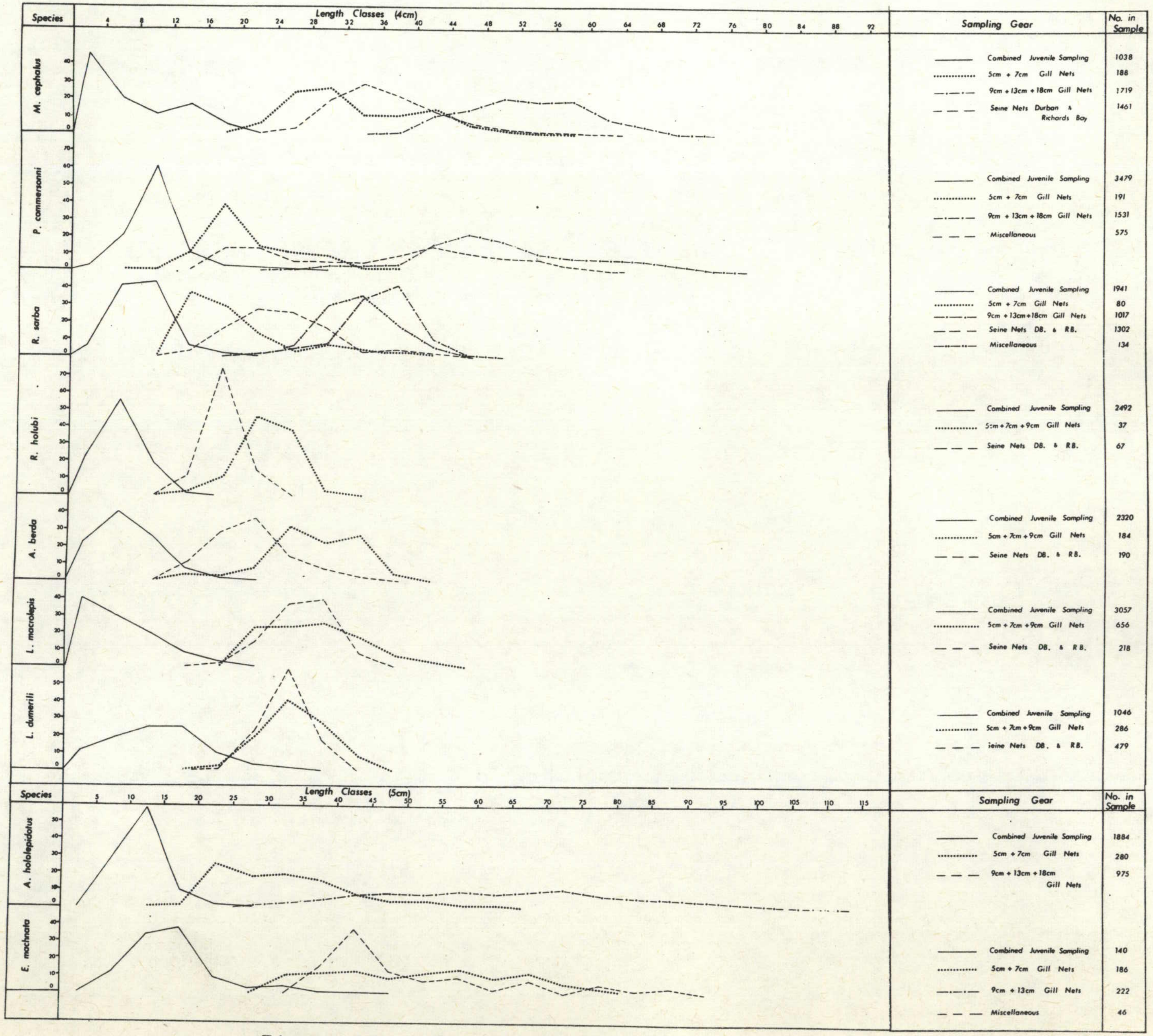


Figure 14. Selectivity of sampling gear

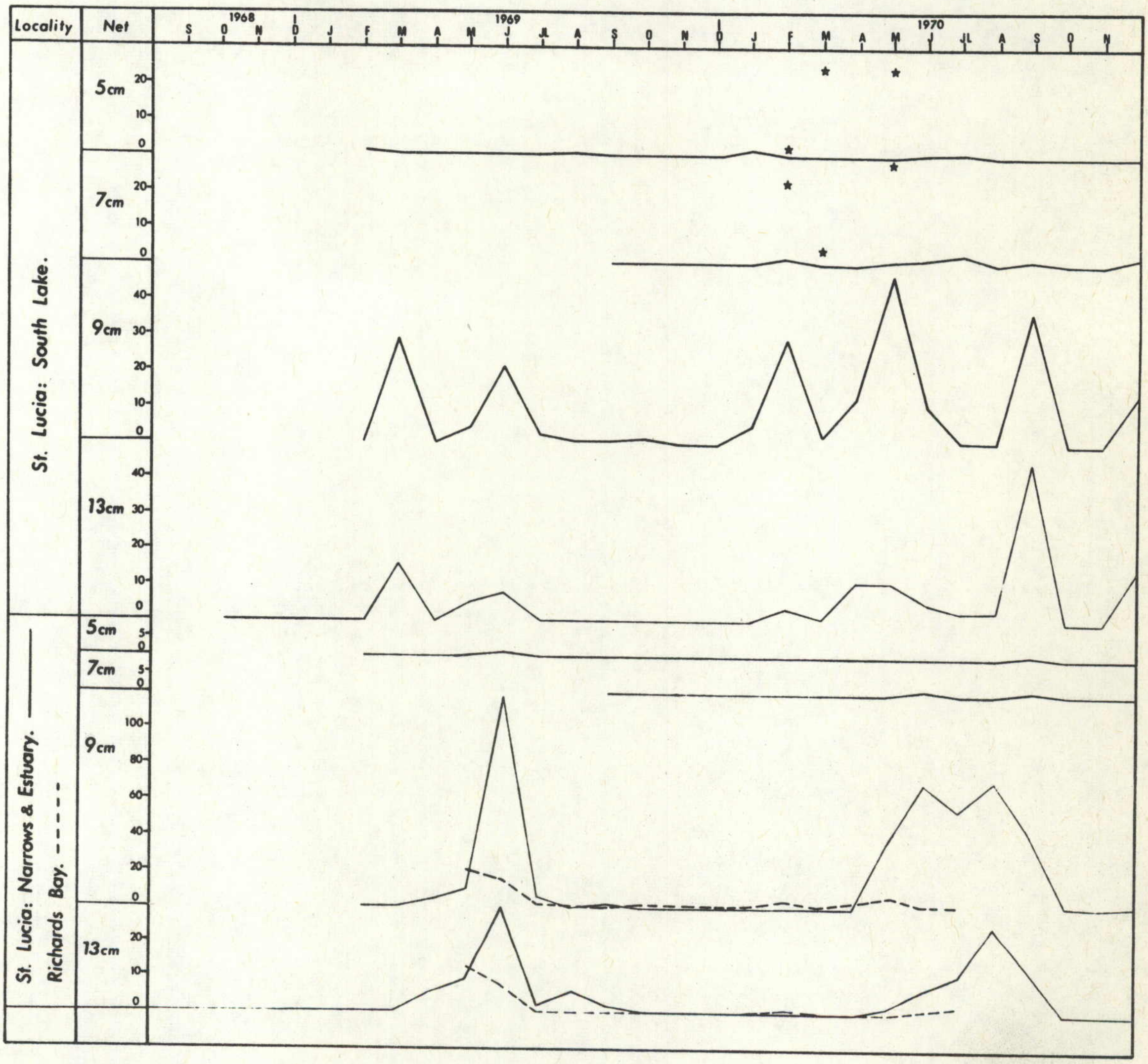


Figure 15. Gill net catches of M. cephalus expressed in terms of catch per 24 hours.

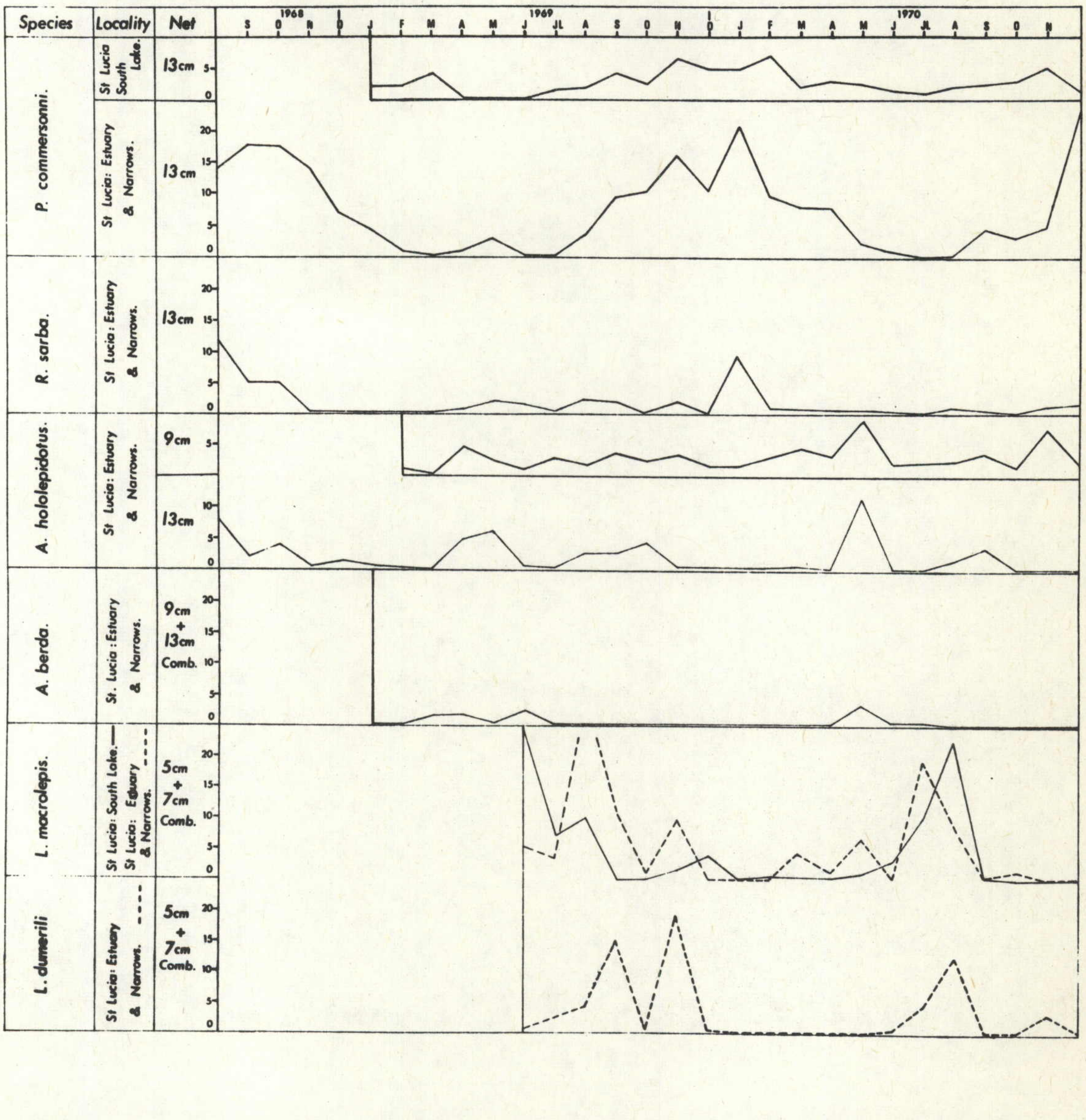


Figure 16. Gill net catches of main estuarine species expressed in terms of catch per 24 hours.

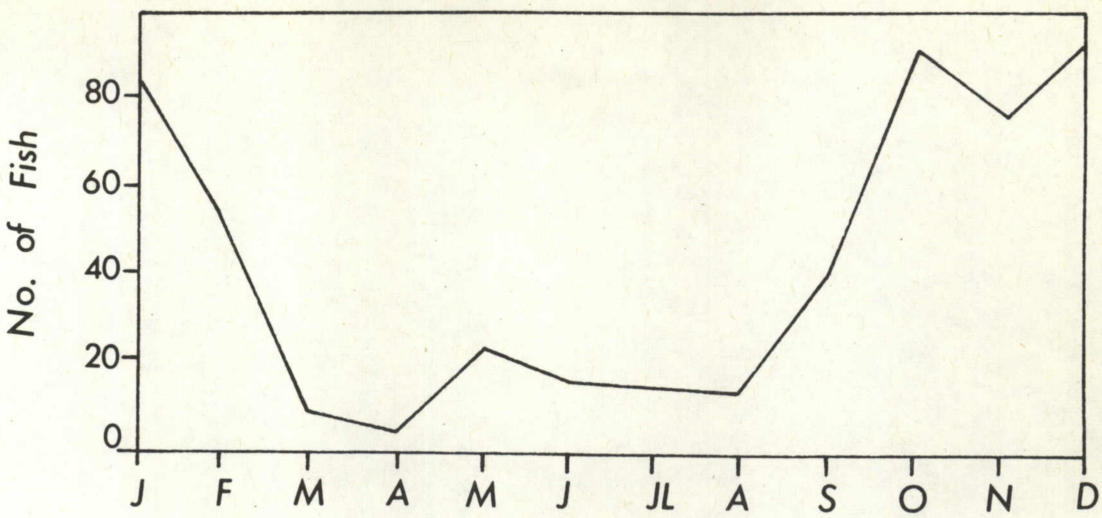


Figure 17. Monthly samples of <u>Pomadasys commersonni</u> obtained from shore anglers in the Durban area (1972 and 1973 data combined; N=523)

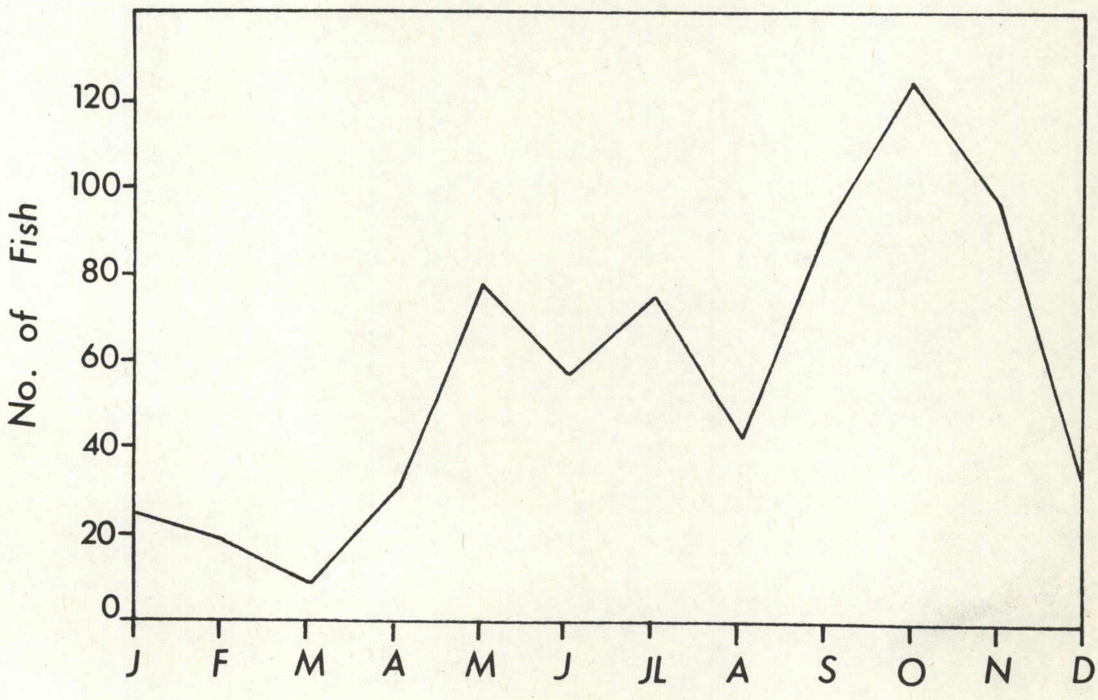


Figure 18. Monthly samples of <u>Rhabdosargus sarba</u> obtained from shore anglers on the Natal coast (1972 and 1973 data combined; N=683).

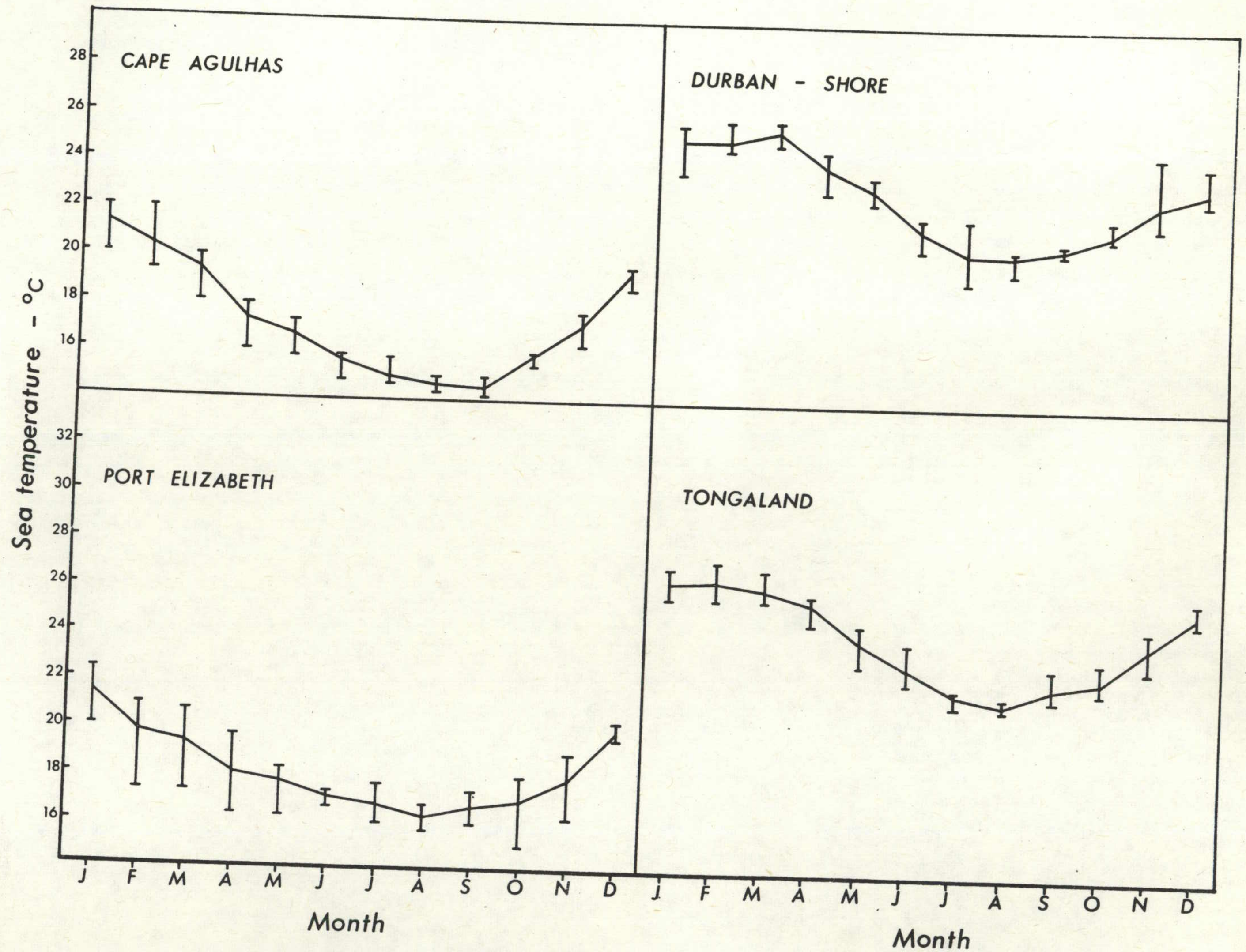


Figure 19. Mean monthly sea surface temperatures derives from synoptic temperature charts issued by the maritime weather office (after Hughes, 1974).

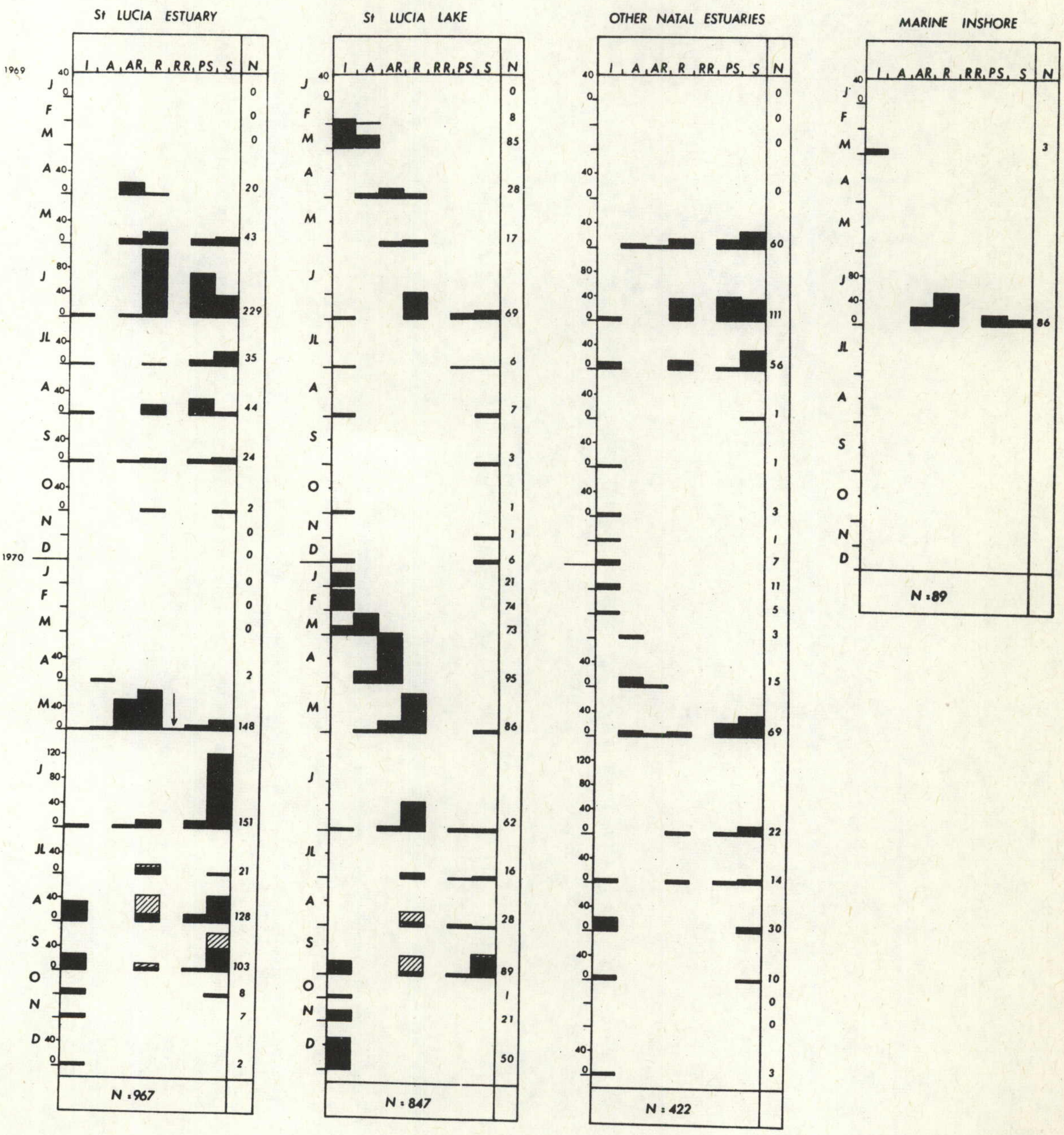


Figure 20. Frequency of occurrence of each stage of gonad development in total monthly samples of sexually mature Mugil cephalus (sexes combined, actual number of specimens plotted).

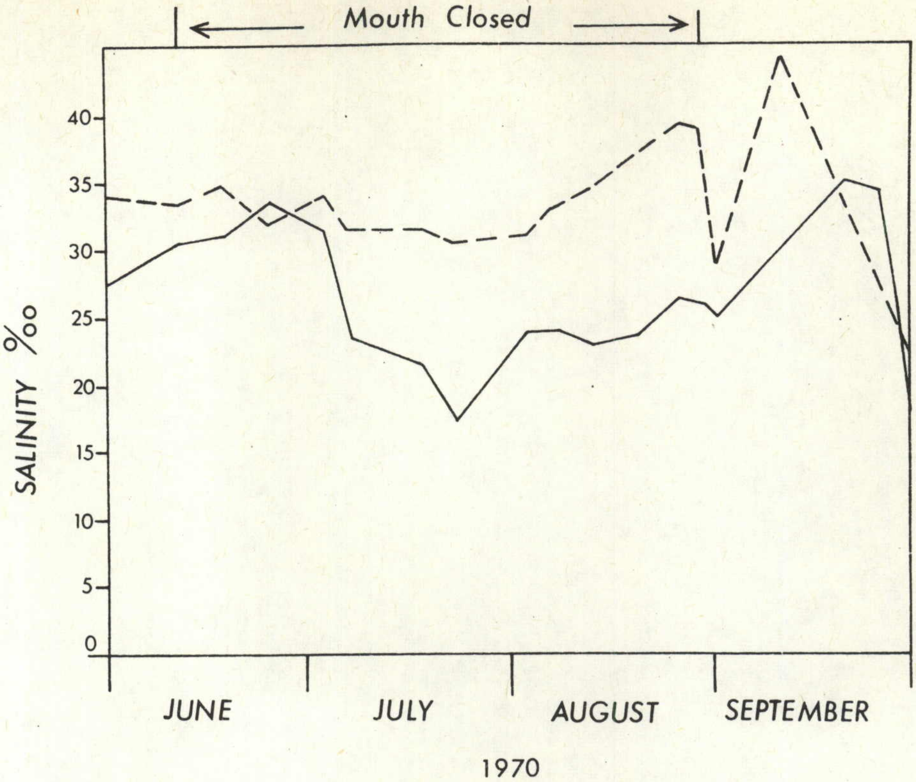


Figure 21. Salinities in the St. Lucia Narrows during the period of closure of the mouth. ——— 5km from the sea - - - - - 20km from the sea

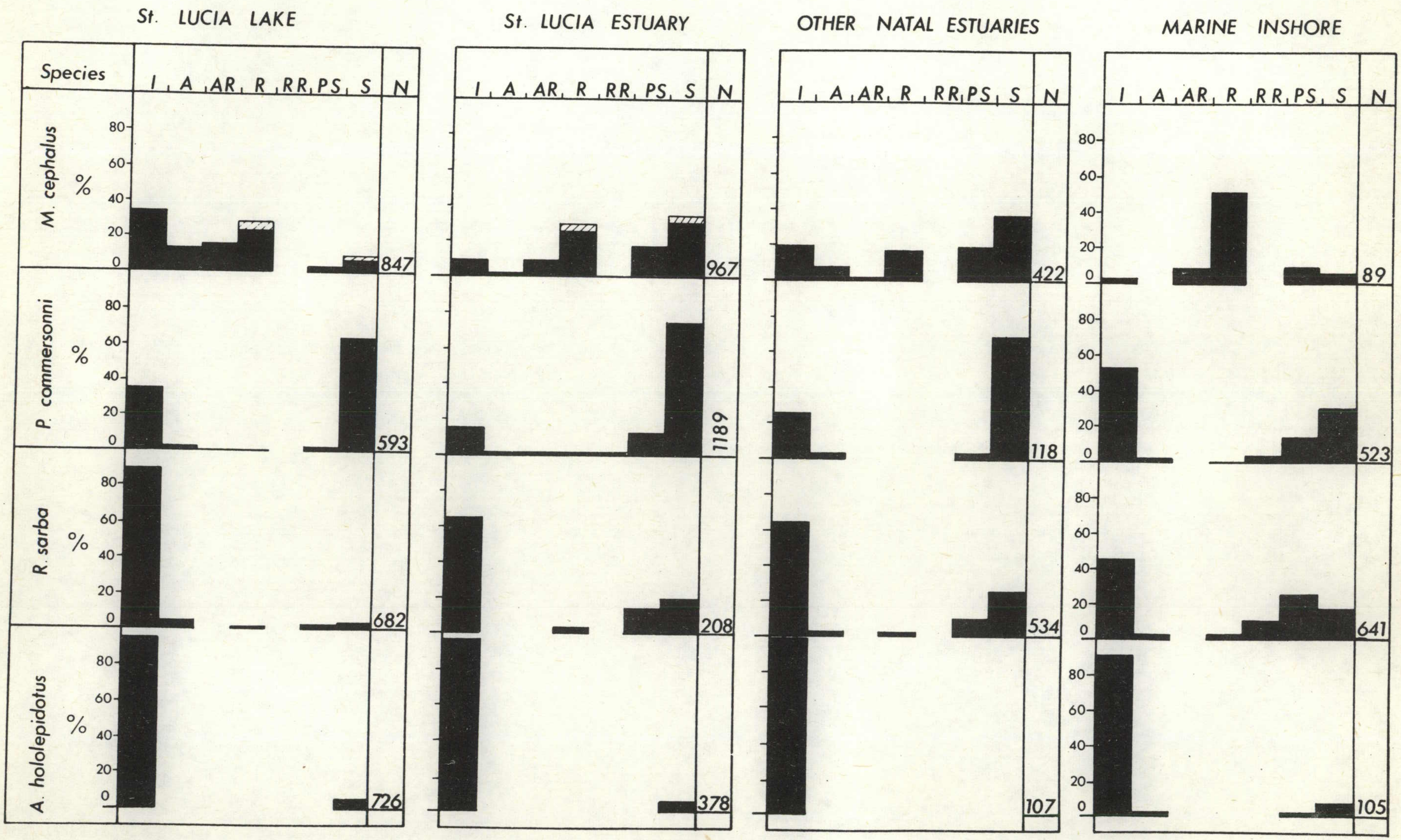


Figure 22. Percentage frequency of occurrence of each stage of gonad development in the total catch obtained from the different sampling areas.

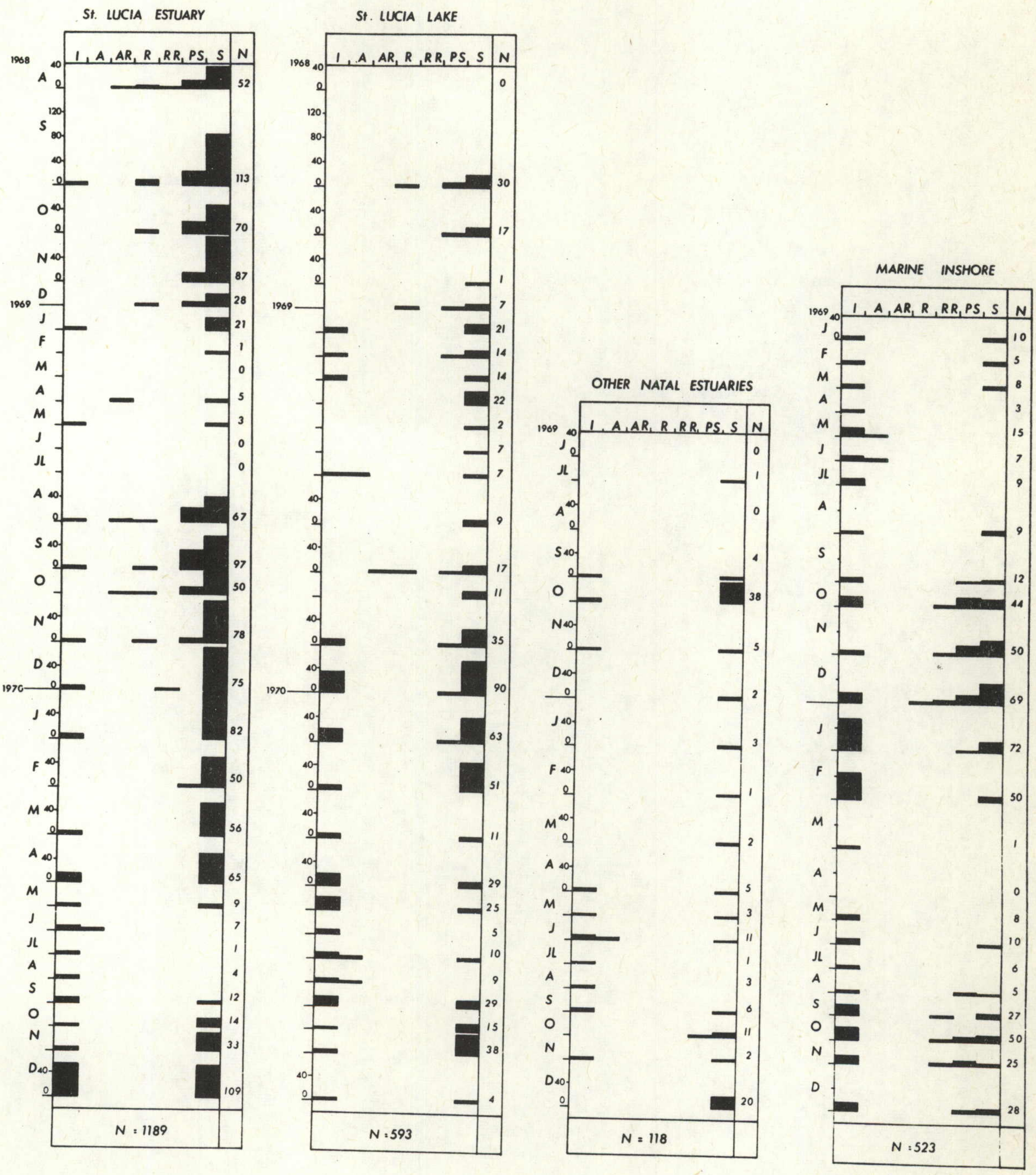


Figure 23. Frequency of occurrence of each stage of gonad development in total monthly samples of sexually mature Pomadasys commersonni (sexes combined, actual number of specimens plotted).

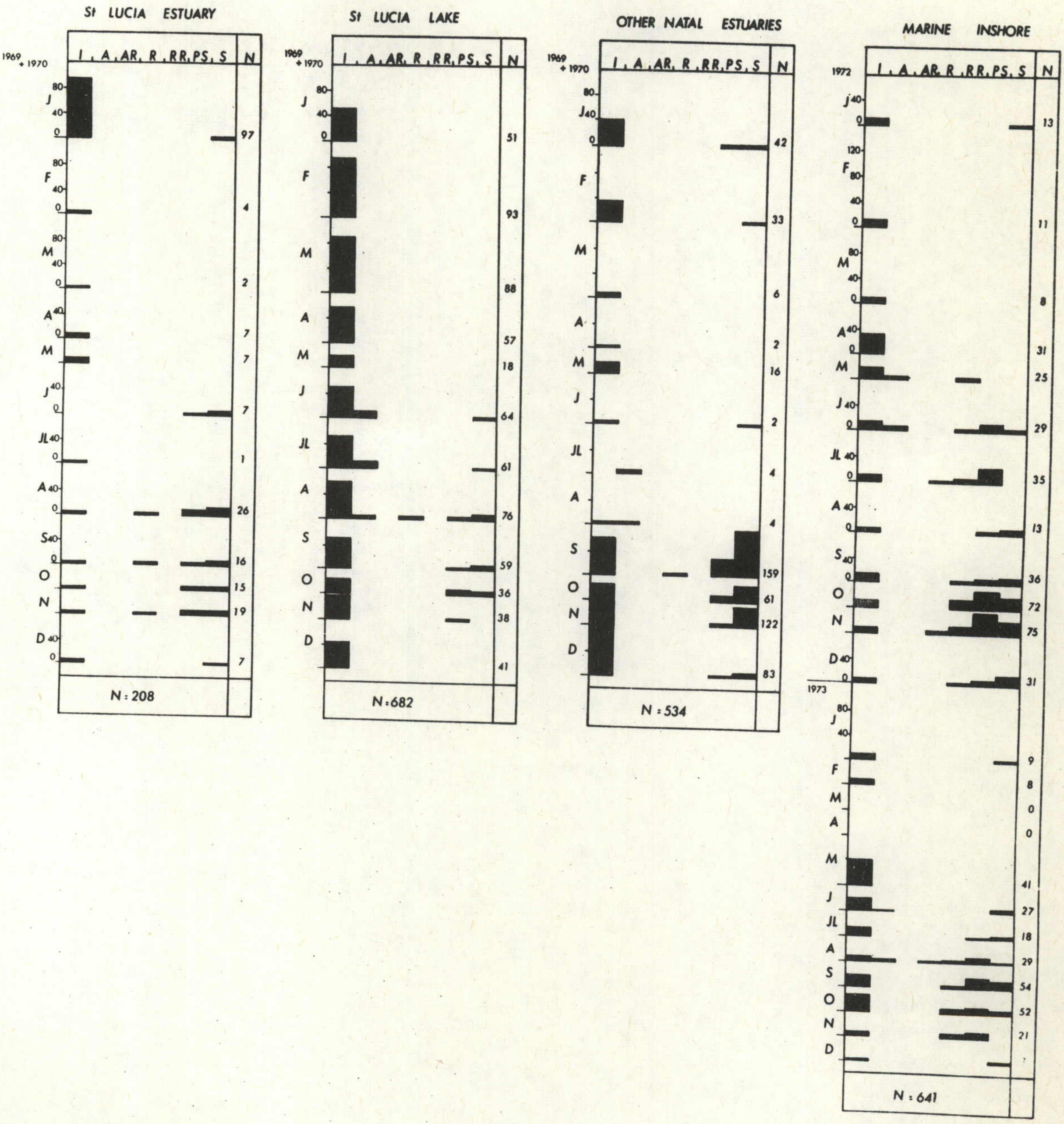


Figure 24. Frequency of occurrence of each stage of gonad development in total monthly samples of sexually mature <u>Rhabdosargus sarba</u> (sexes combined, actual number of specimens plotted).

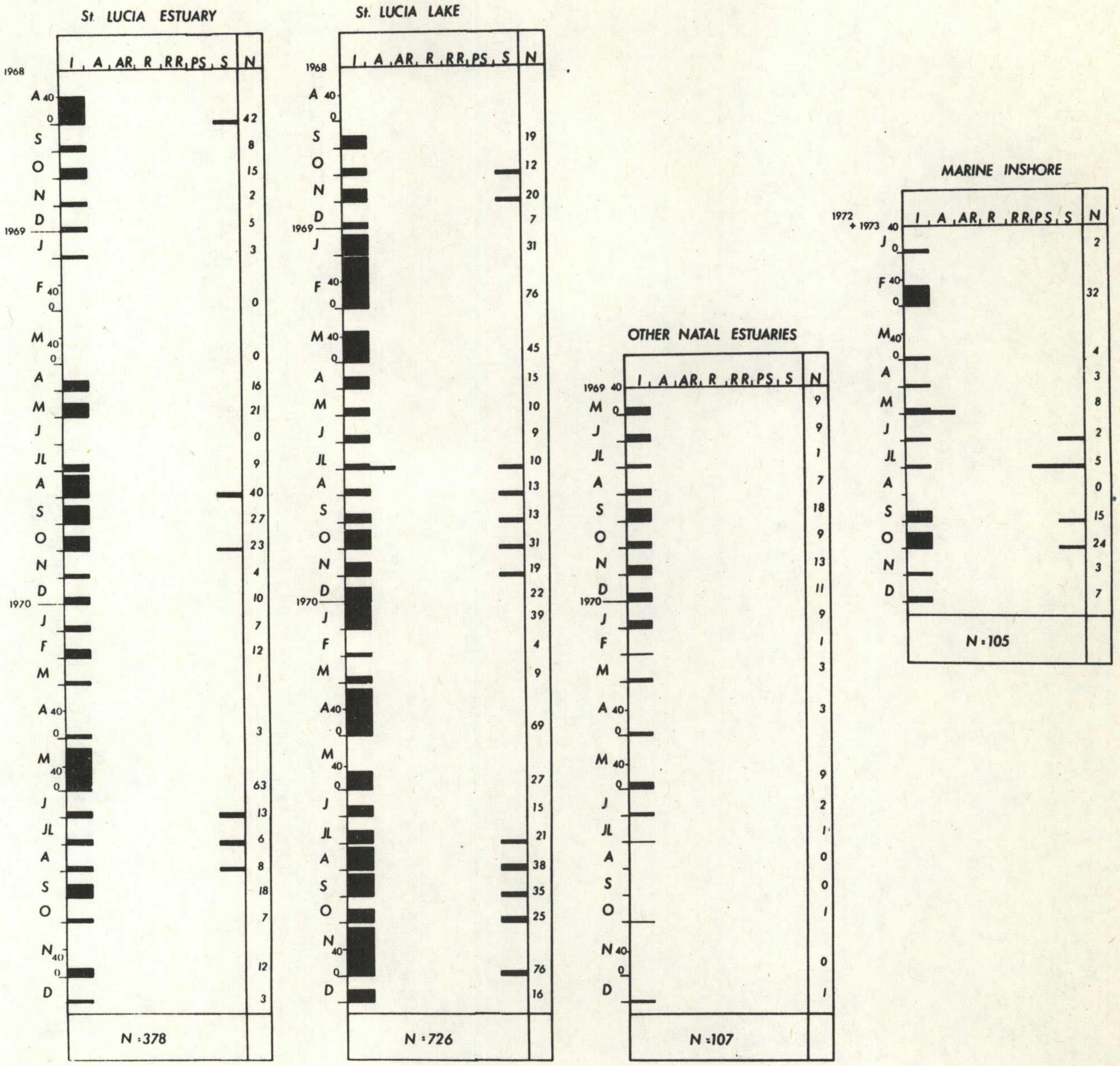


Figure 25. Frequency of occurrence of each stage of gonad development in total monthly samples of sexually mature *Argyrosomus hololepidotus* (sexes combined, actual number of specimens plotted).

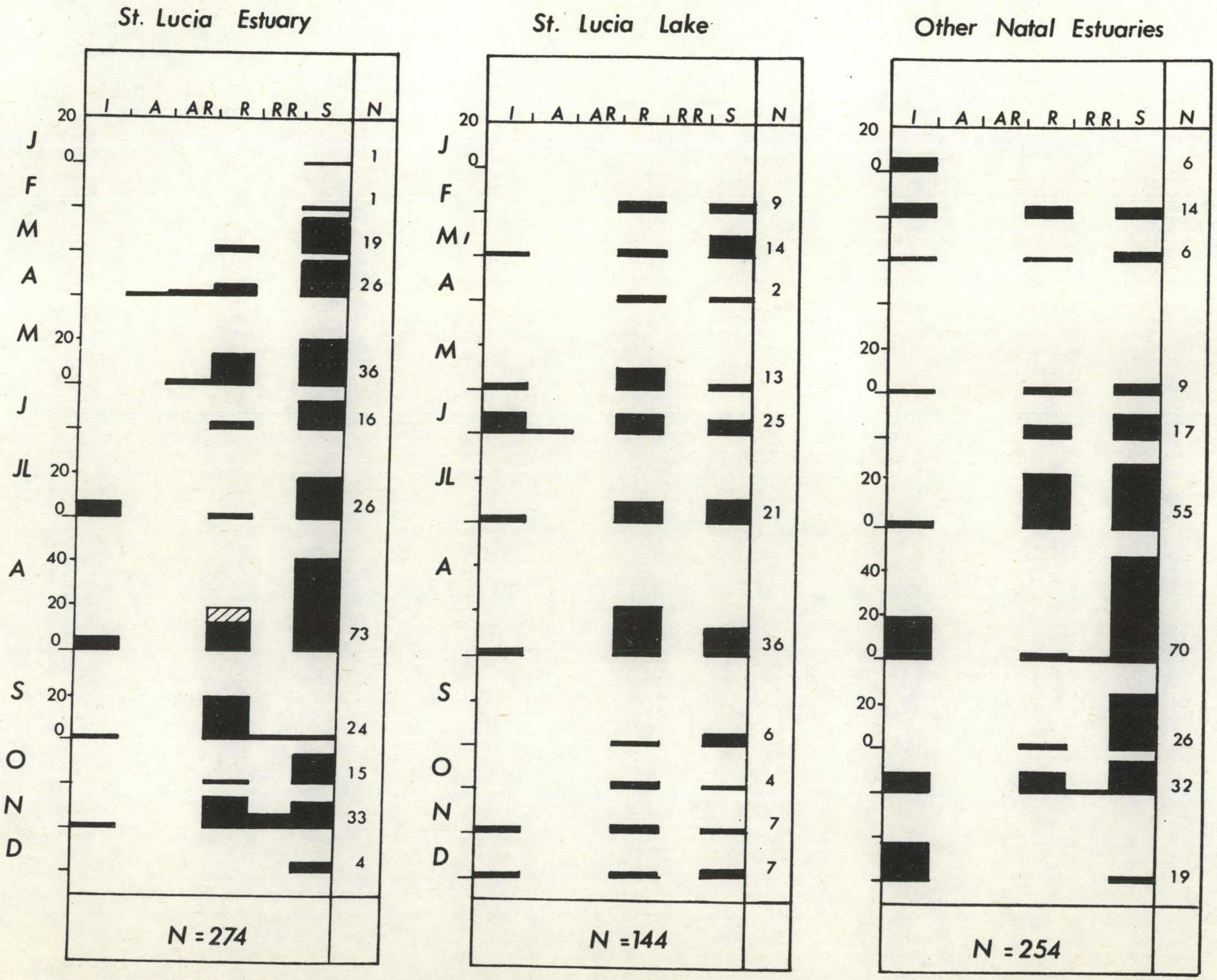


Figure 26. Frequency of occurrence of each stage of gonad development in total monthly samples of sexually mature <u>Liza macrolepis</u> (sexes combined, actual number of specimens plotted).

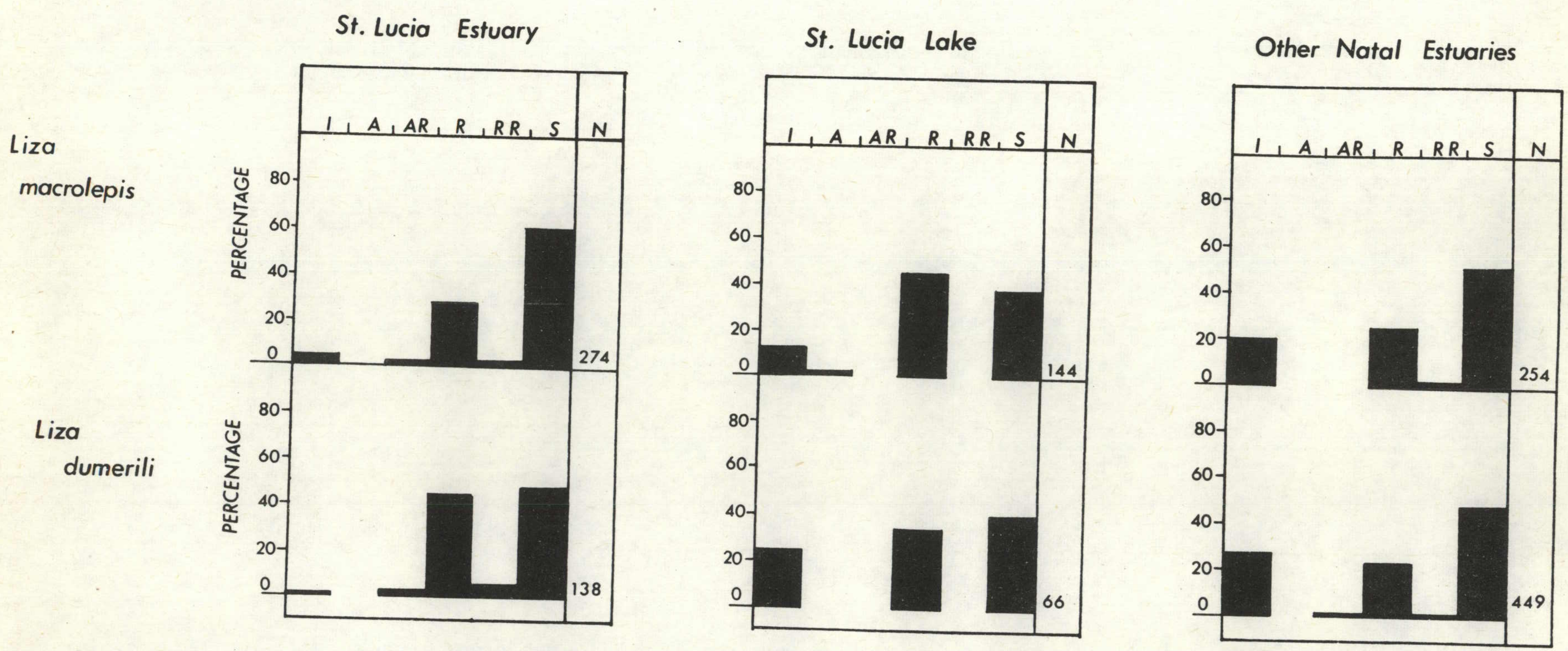


Figure 27. Percentage frequency of occurrence of each stage of gonad development in the total catch of <u>Liza macrolepis</u> and <u>L. dumerili</u> obtained from the different estuarine sampling areas.

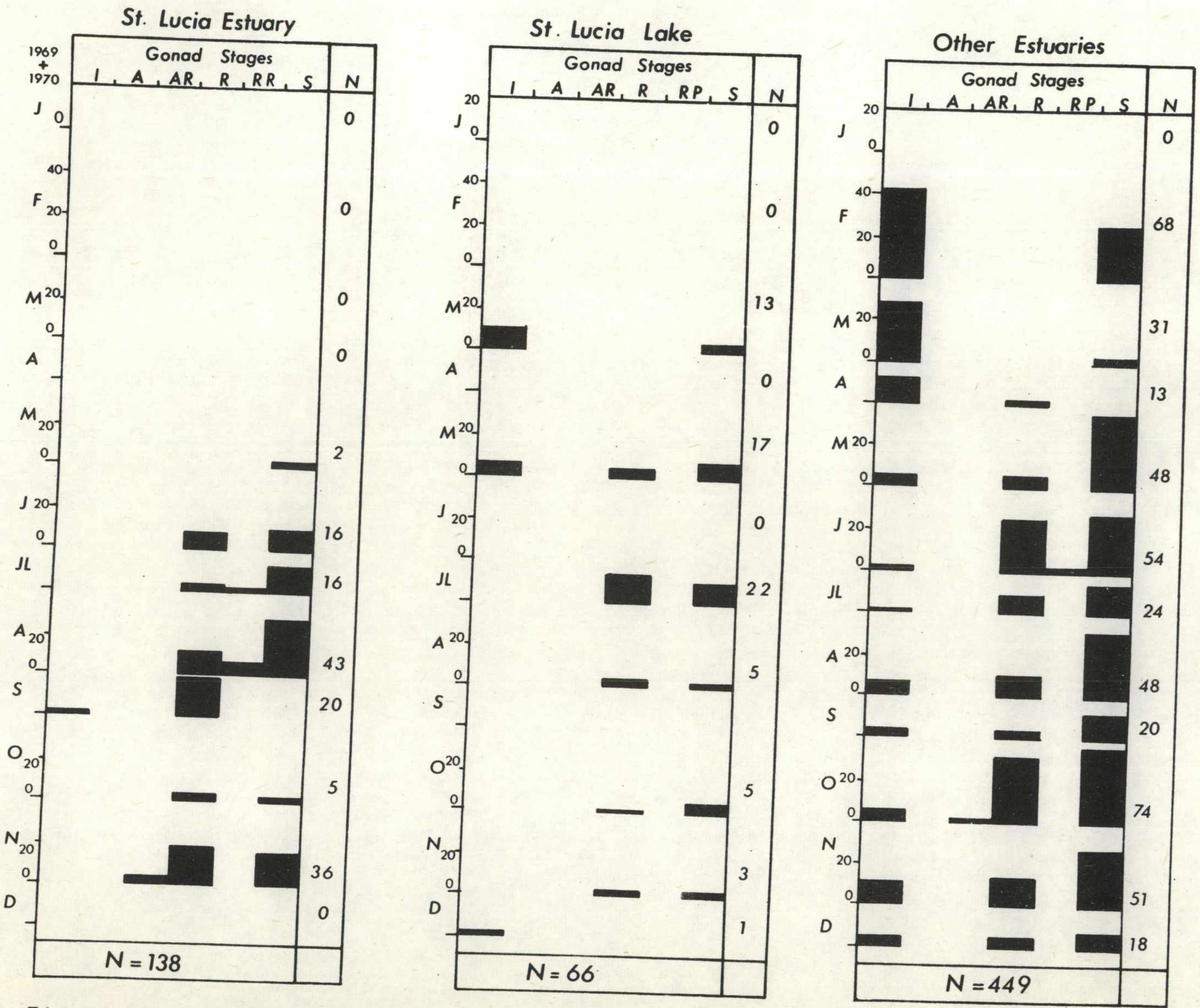


Figure 28. Frequency of occurrence of each stage of gonad development in total monthly samples of sexually mature Liza dumerili (sexes combined, actual number of specimens plotted)

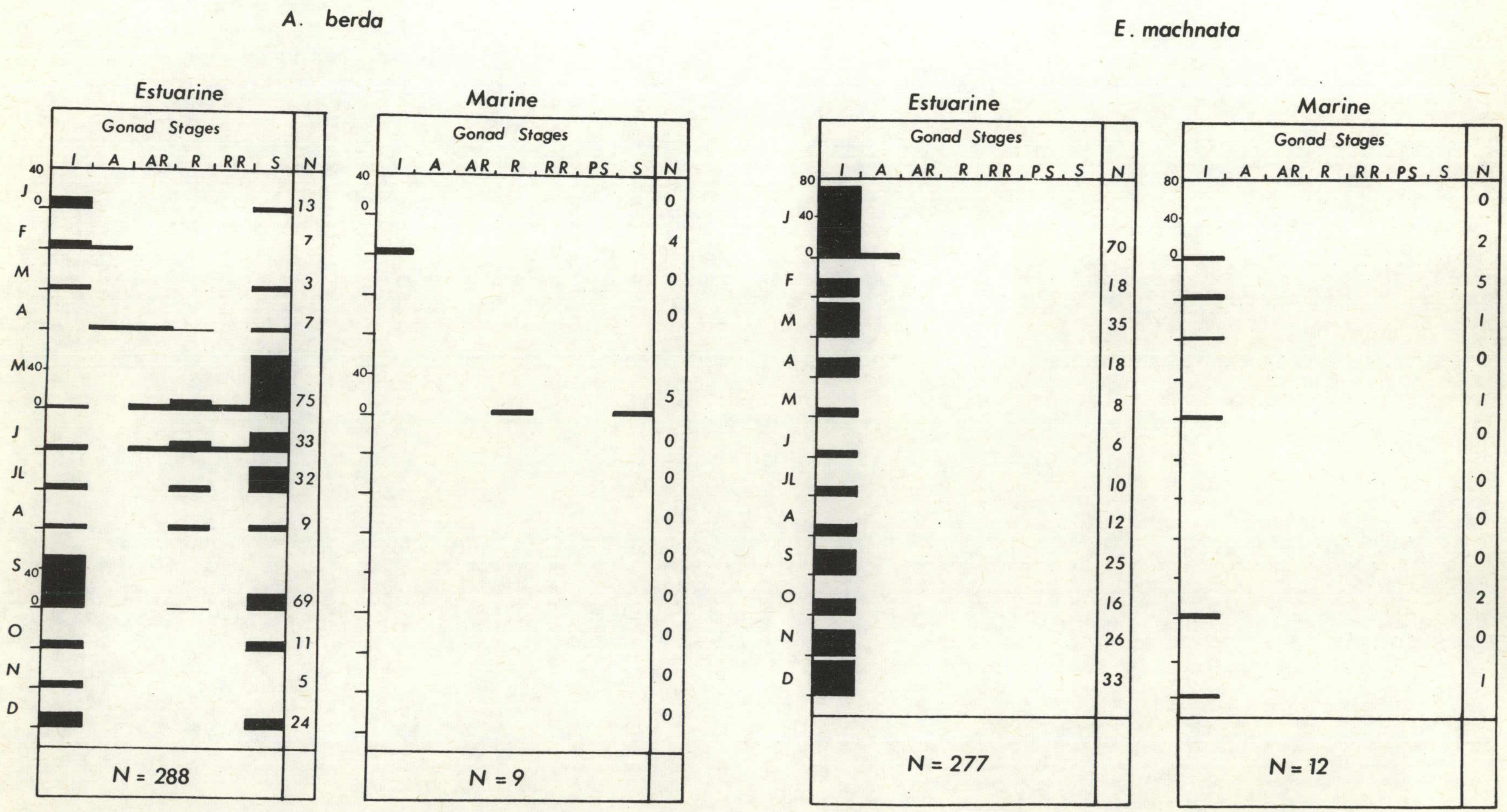


Figure 29. Frequency of occurrence of each stage of gonad development in total monthly samples of *Acanthopagrus berda* and *Elops machnata* (sexes combined, actual number of specimens plotted).

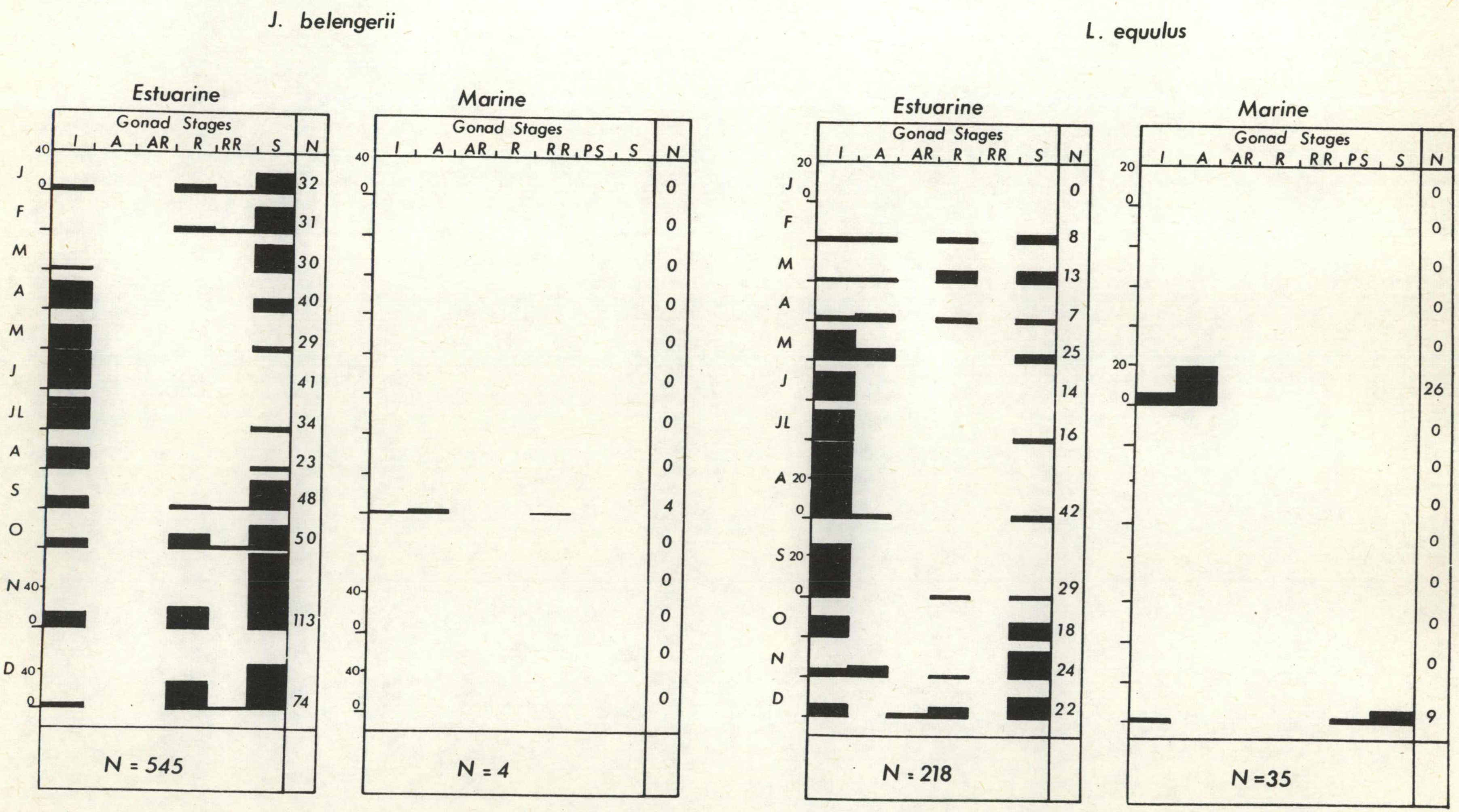


Figure 30. Frequency of occurrence of each stage of gonad development in total monthly samples of <u>Johnius belengerii</u> and <u>Leiognathus equulus</u> (sexes combined, actual number of specimens plotted).

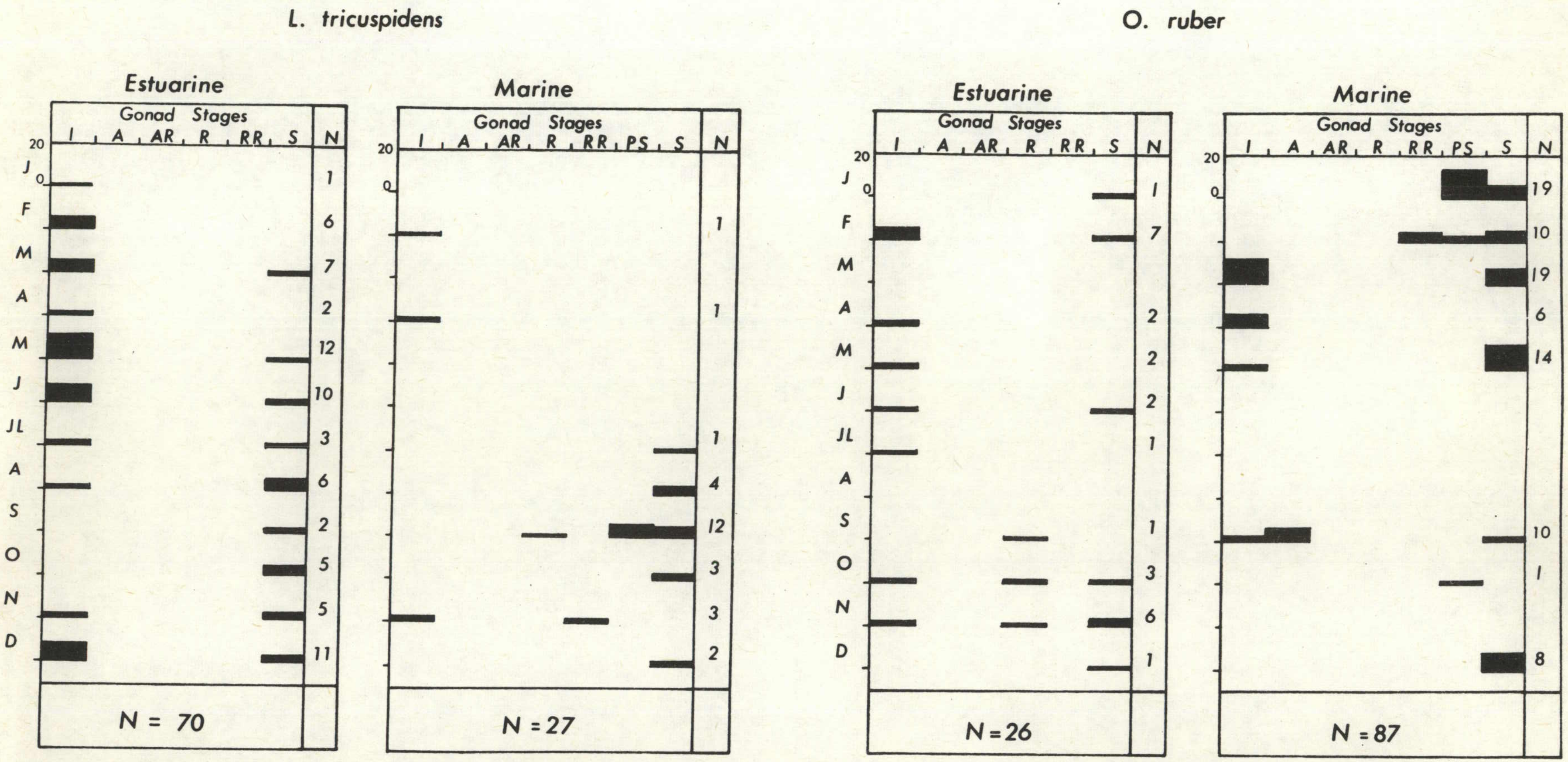


Figure 31. Frequency of occurrence of each stage of gonad development in total monthly samples of <u>Liza tricuspidens</u> and <u>Otolithes ruber</u> (sexes combined, actual number of specimens plotted).

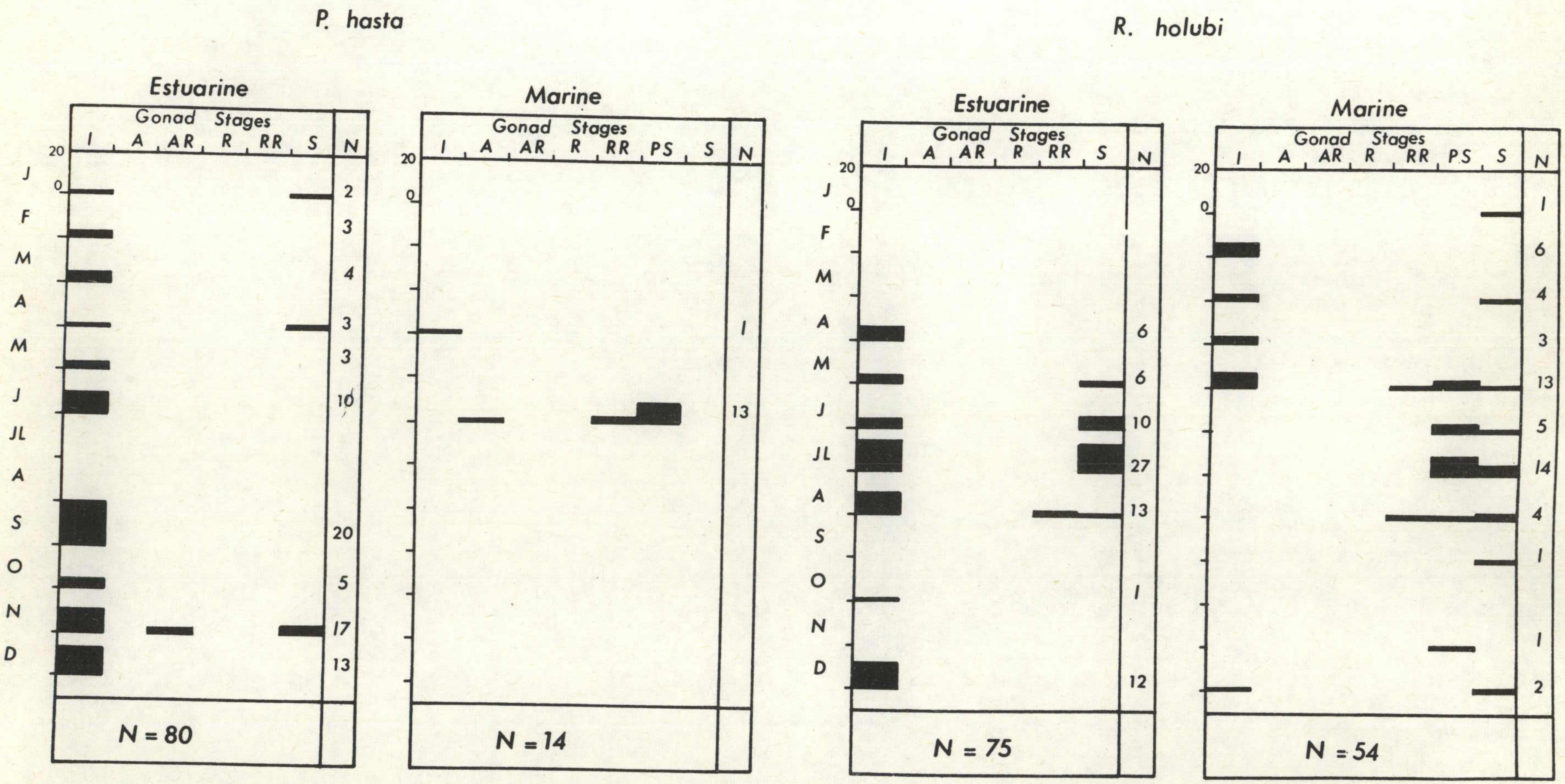


Figure 32. Frequency of occurrence of each stage of gonad development in total monthly samples of Pomadasys hasta and Rhabdosargus holubi (sexes combined, actual number of specimens plotted).

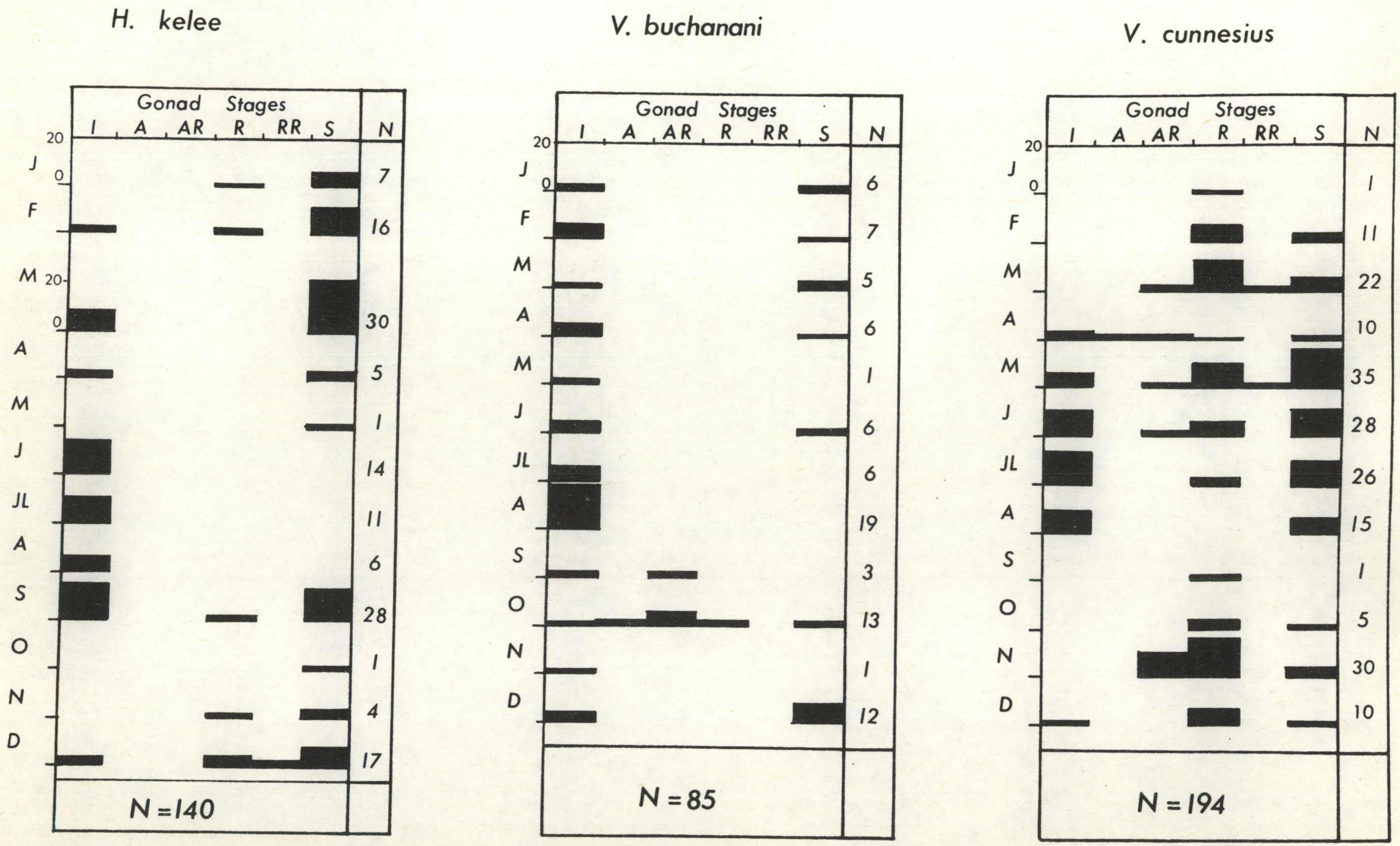


Figure 33. Frequency of occurrence of each stage of gonad development in total monthly estuarine samples of <u>Hilsa kelee</u>, <u>Valalamugil buchanani</u> and <u>V. cunnesius</u> (sexes combined, actual number of specimens plotted).

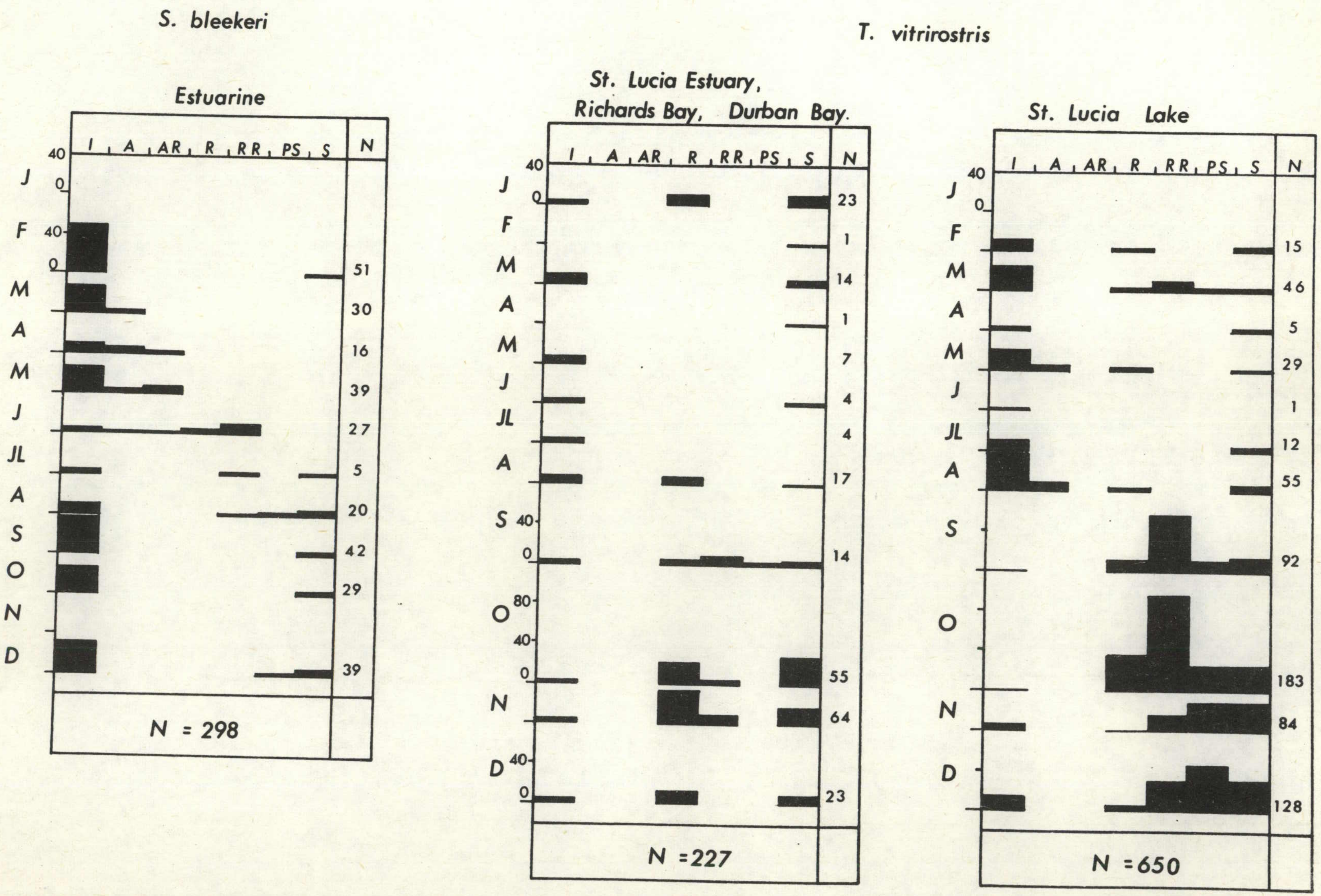


Figure 34. Frequency of occurrence of each stage of gonad development in total monthly samples of <u>Solea bleekeri</u> and <u>Thryssa vitrirostris</u> (sexes combined, actual number of specimens plotted).

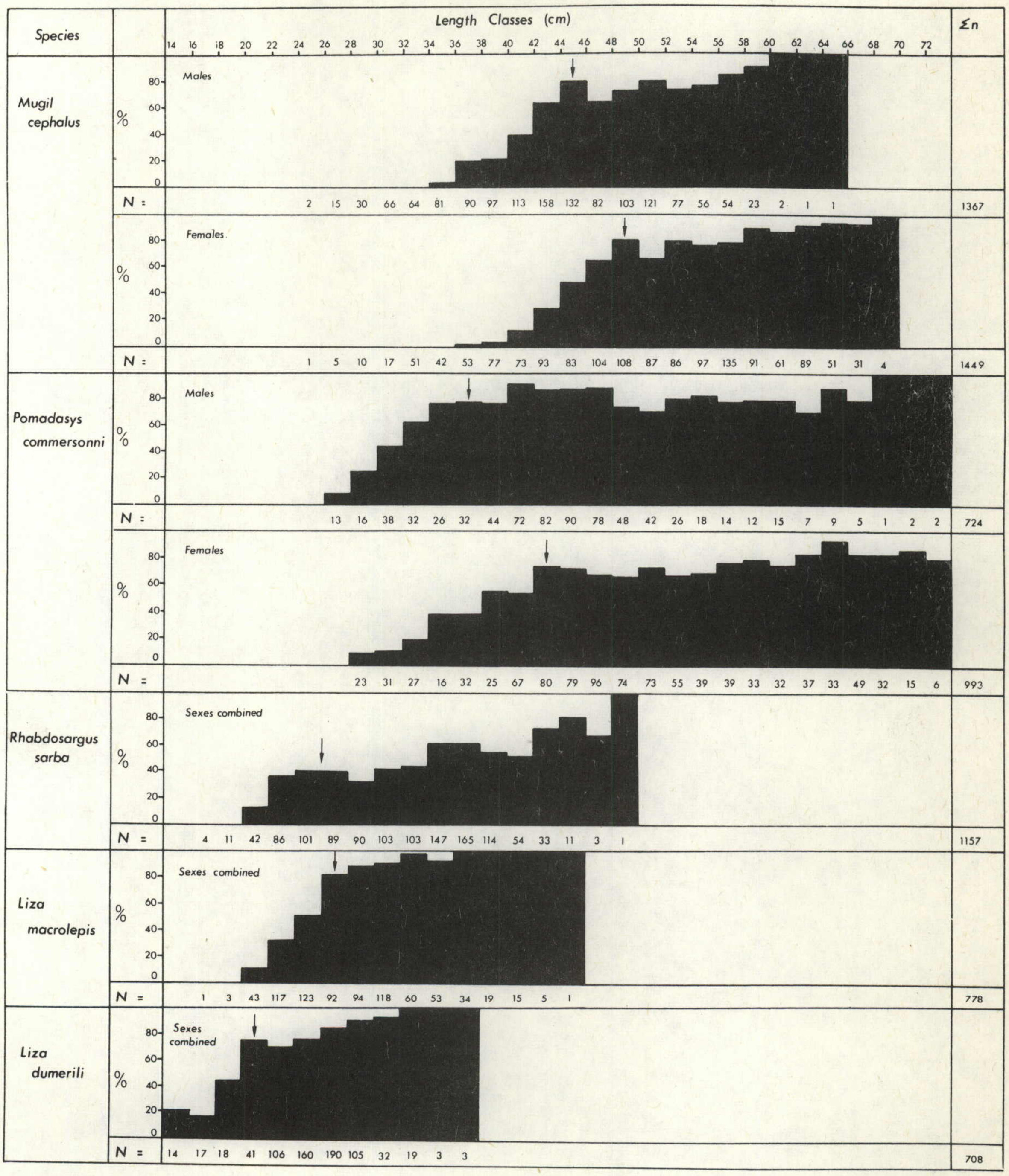


Figure 35. Length of attainment of sexual maturity. In each length class the number of fish with mature gonads (ranging from active to spent condition) has been expressed as a percentage of the total number of fish in that class (including inactives and immatures). Mature gonads active to spent condition ■ Immature/inactive gonads □

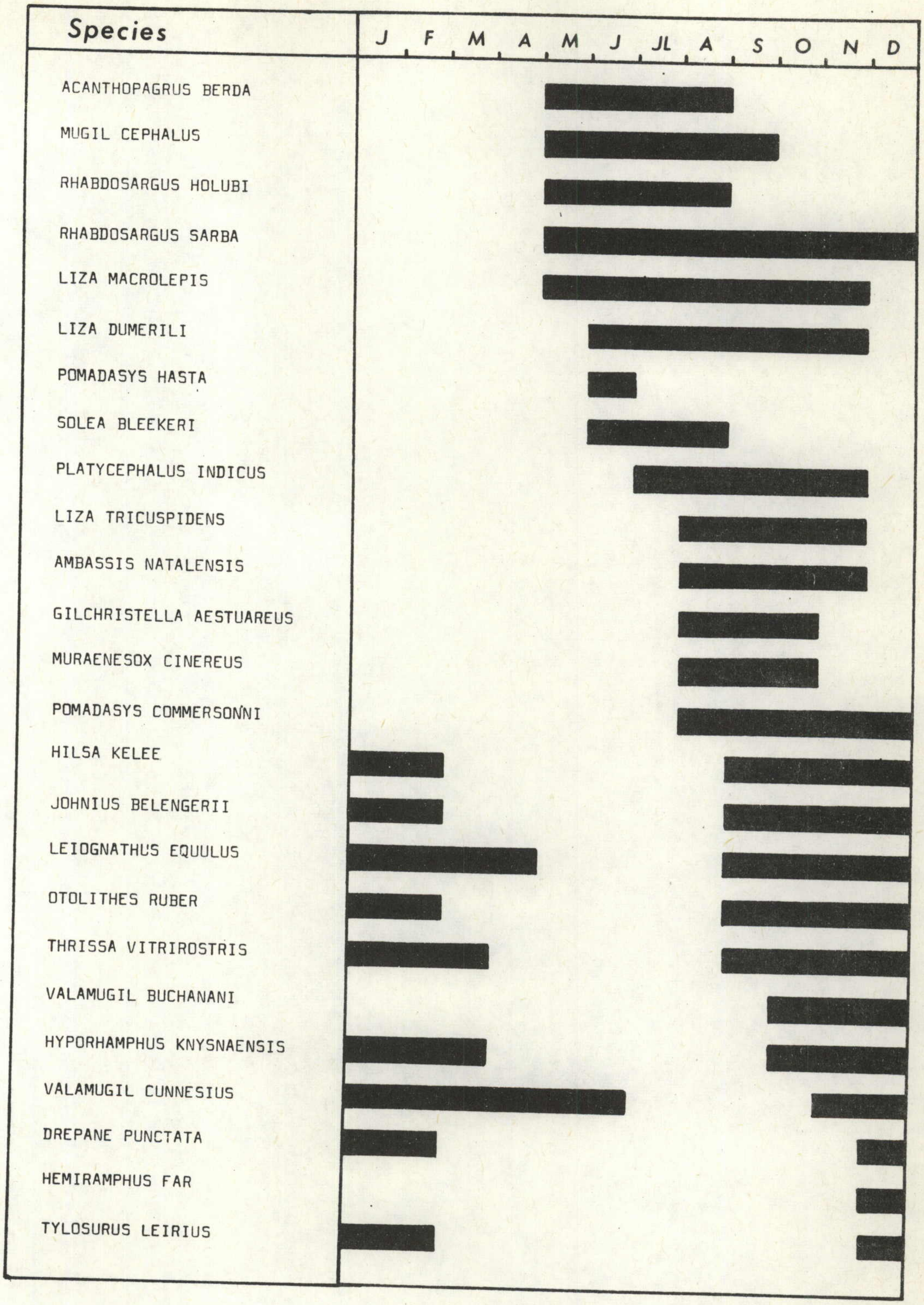


Figure 36. Synoptic presentation of data obtained on months of spawning of fish that occur in Natal estuaries.

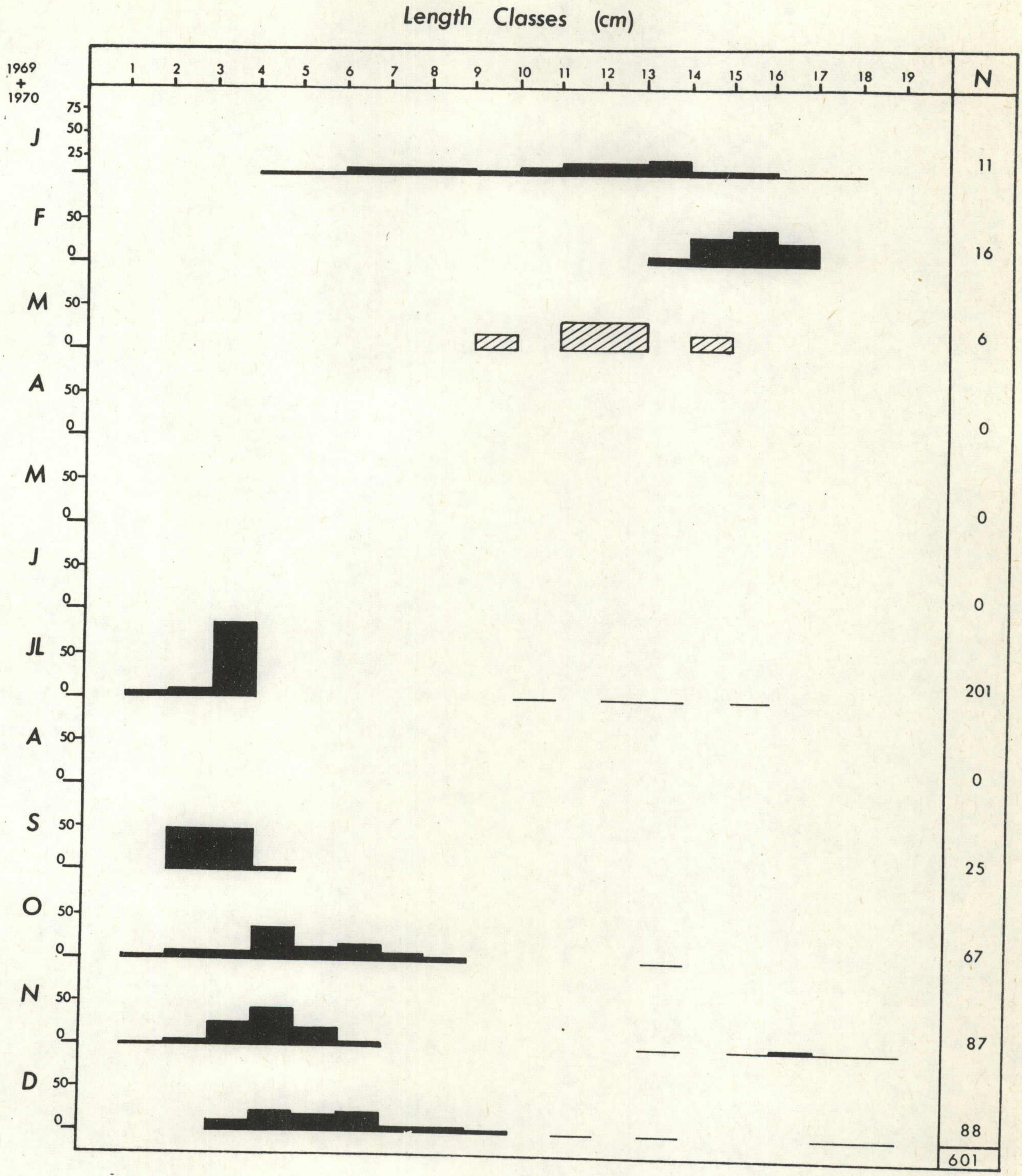


Figure 37. Percentage length composition of monthly catches of juvenile Mugil cephalus (1969 and 1970 data lumped).

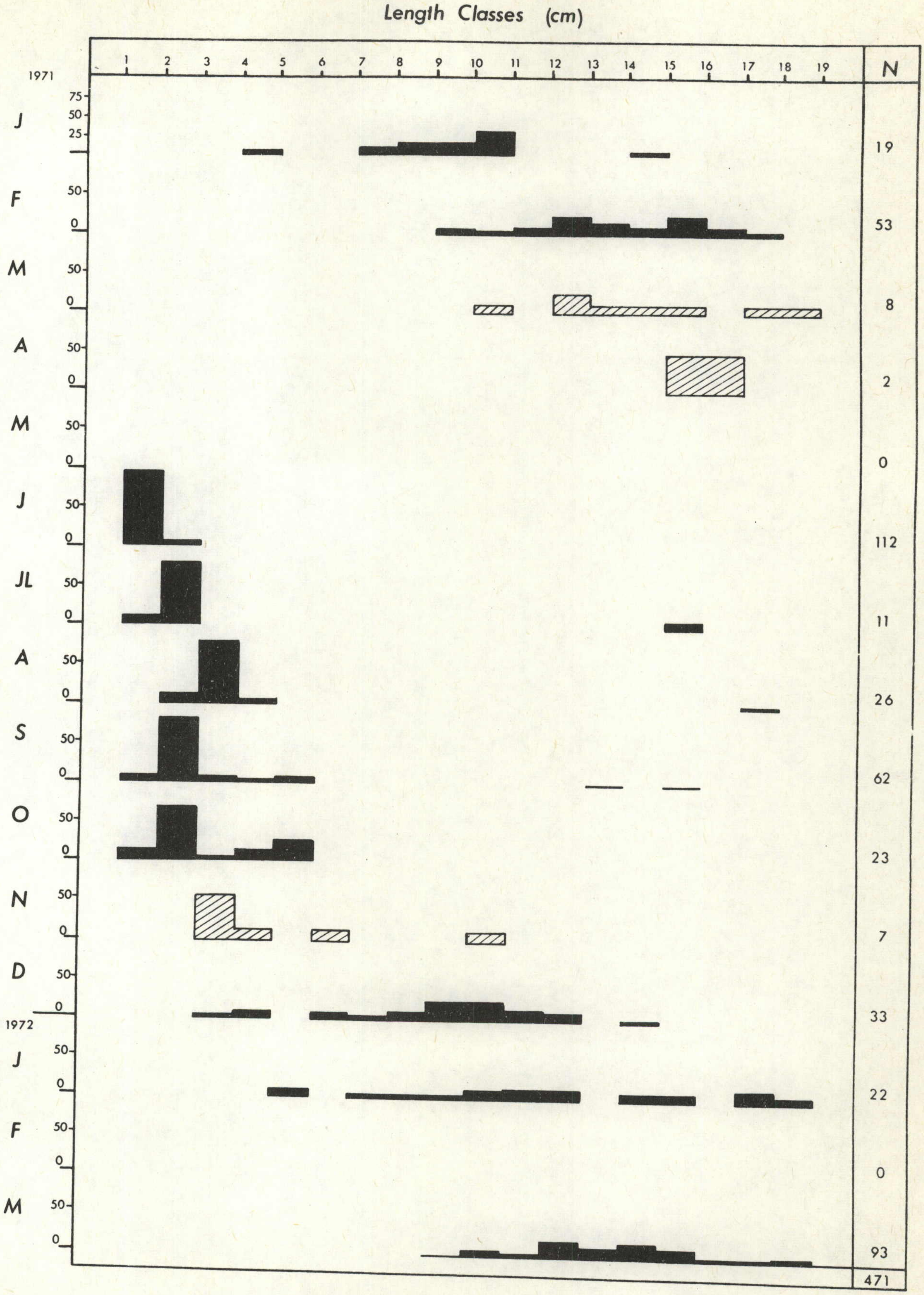


Figure 38. Percentage length composition of monthly catches of juvenile *Mugil cephalus* (1971/72)

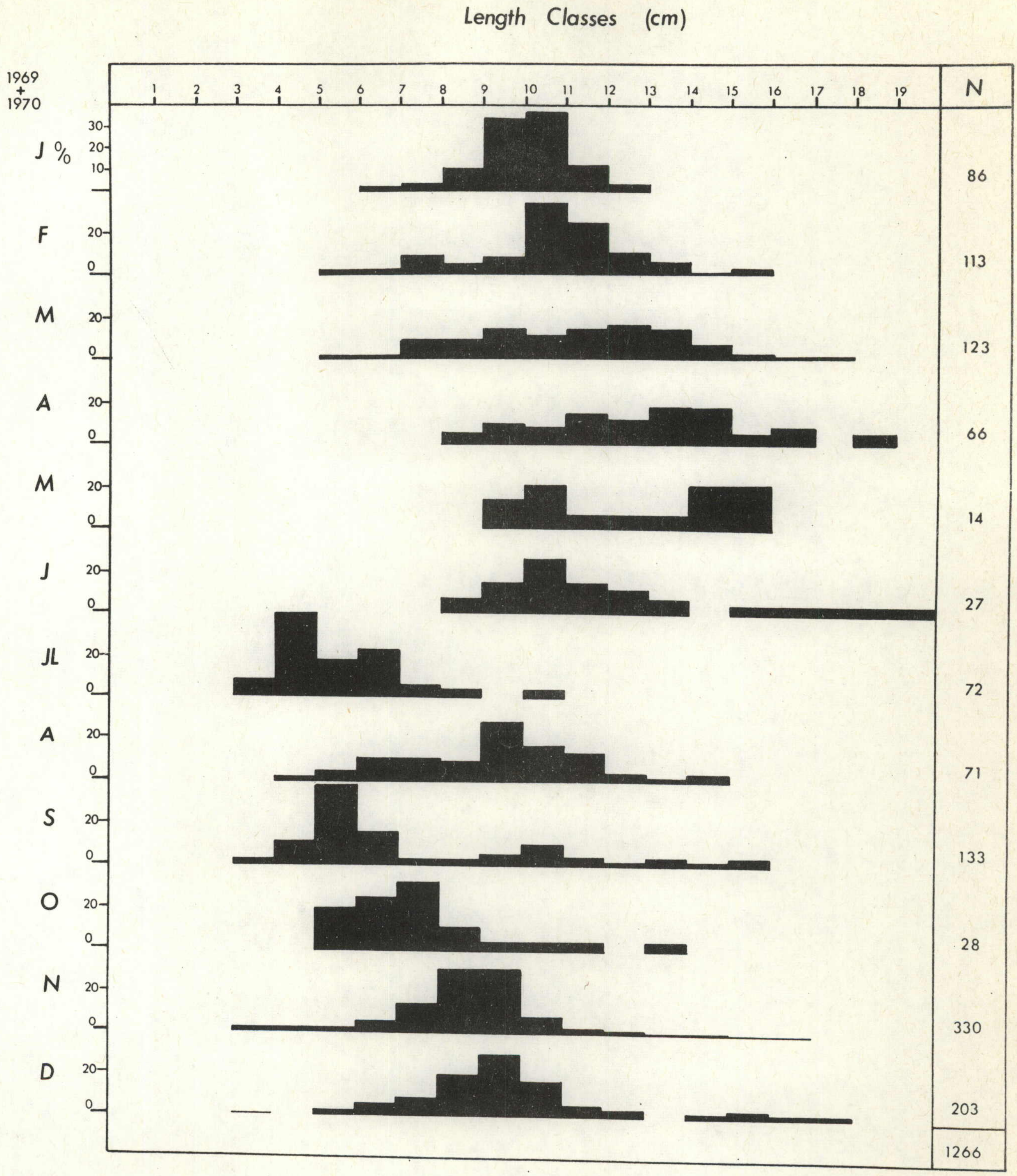


Figure 39. Percentage length composition of monthly catches of juvenile *Pomadasys commersonni* (1969 and 1970 data lumped).

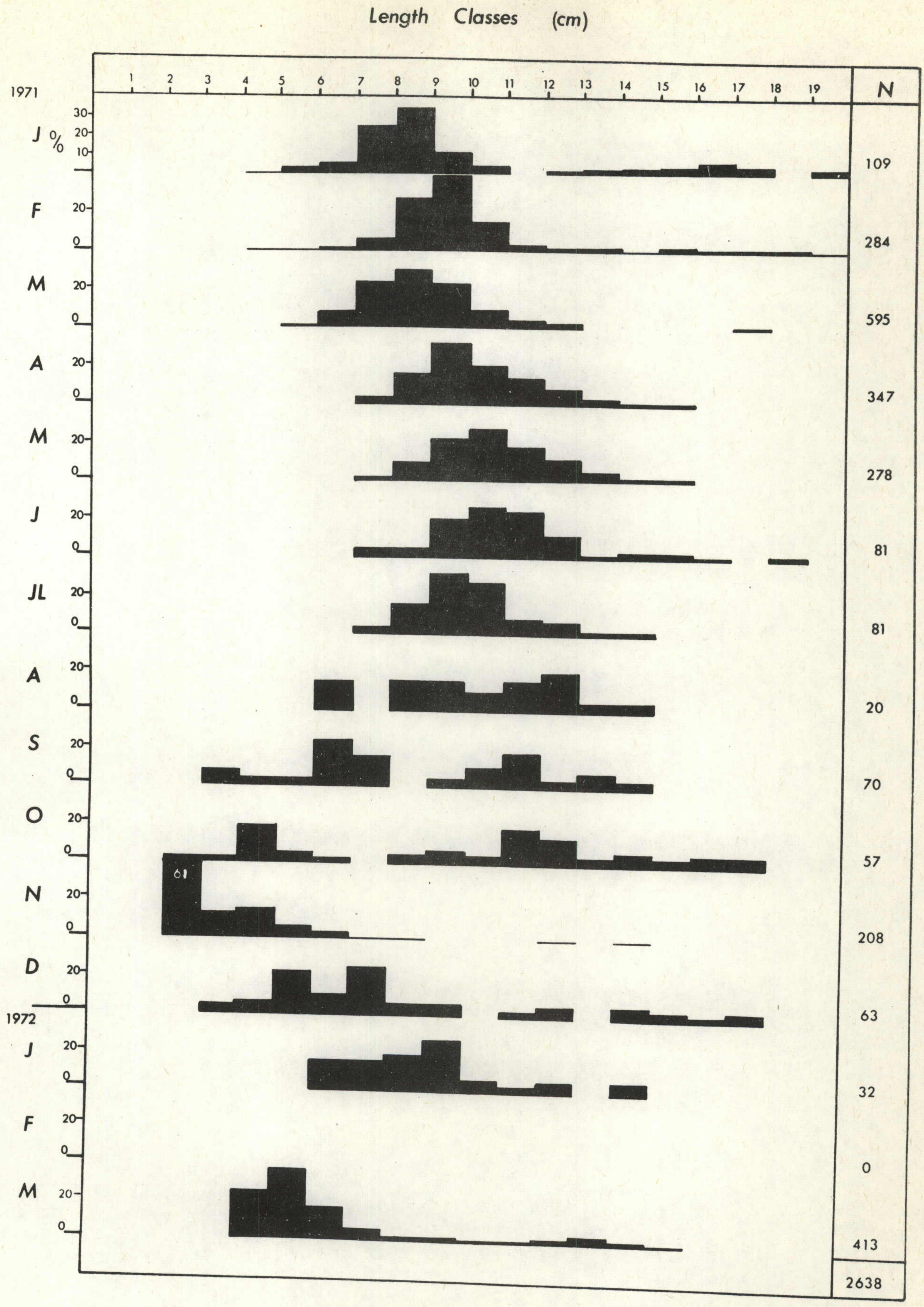


Figure 40. Percentage length composition of monthly catches of juvenile *Pomadasys commersonni* (1971/72).

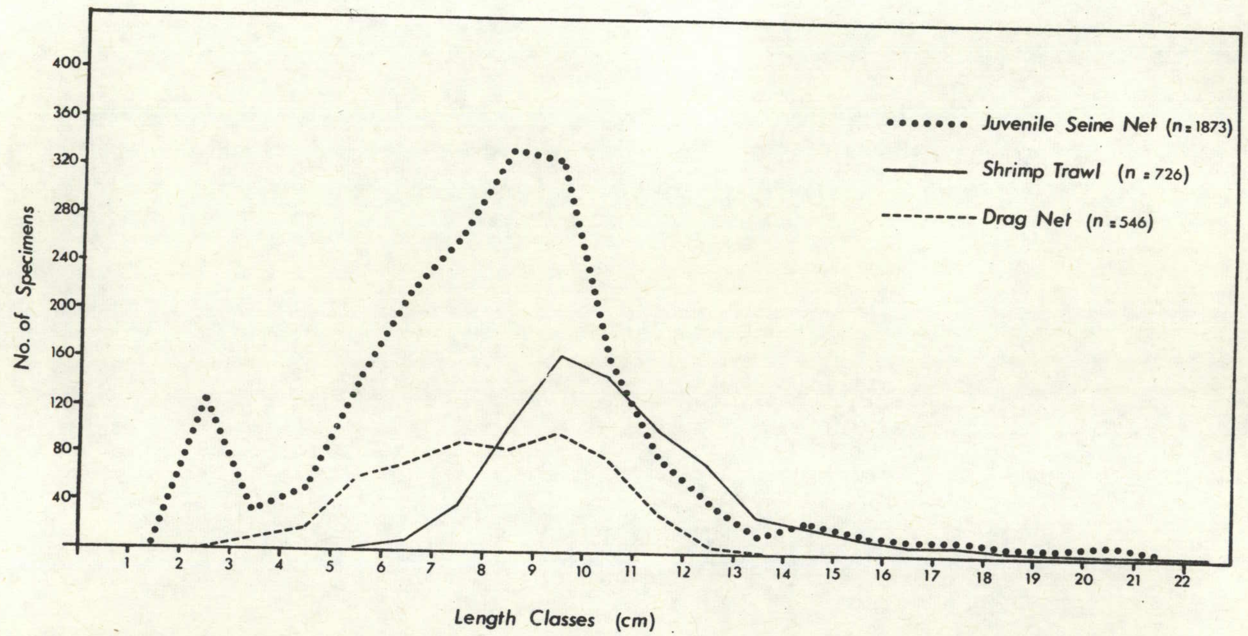


Figure 41. Selectivity of nets used to sample juvenile <u>Pomadasys commersonni</u>

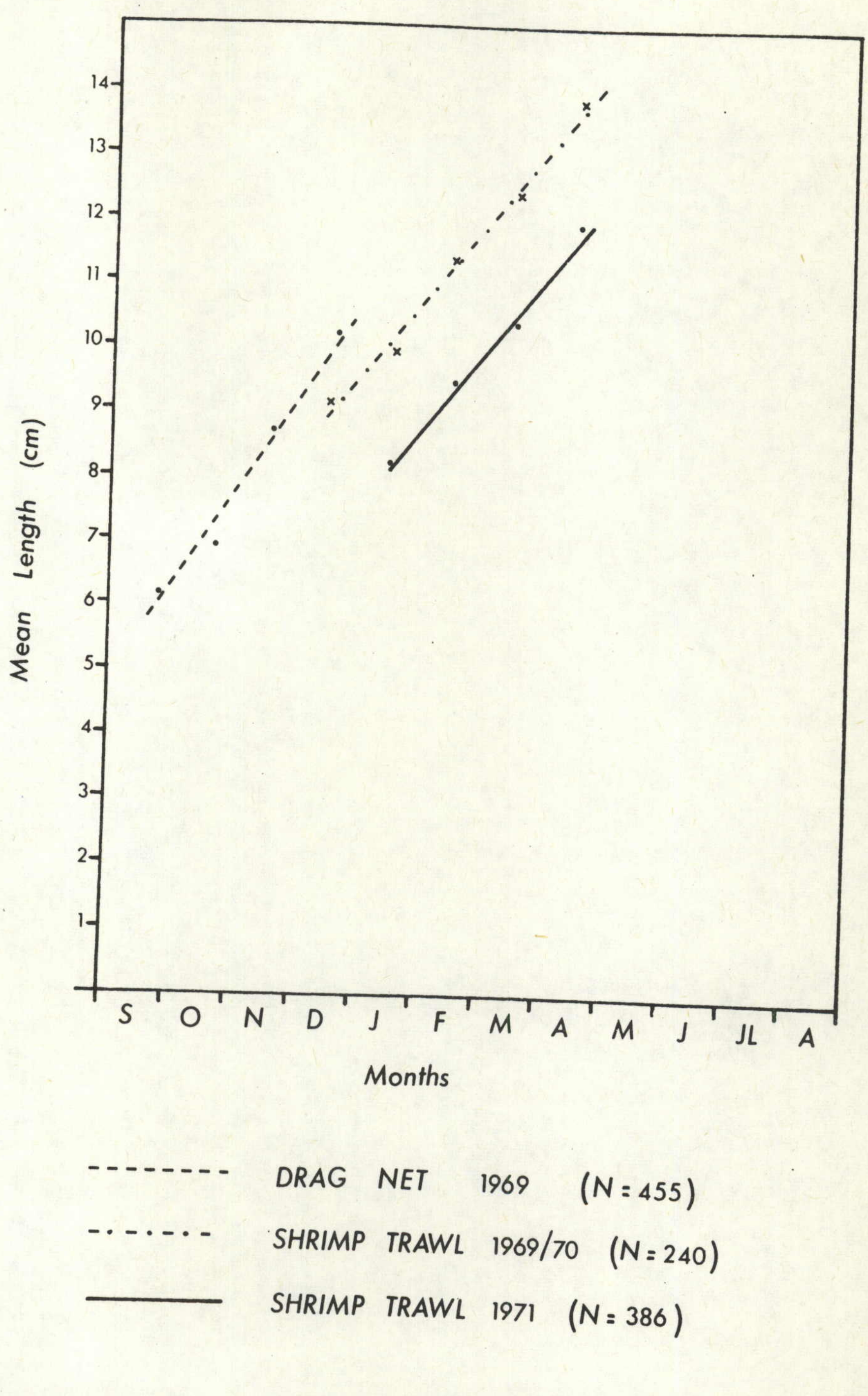


Figure 42. Estimates of rate of growth of juvenile *Pomadasys commersonni* based on the mean lengths of monthly catches taken in different nets.

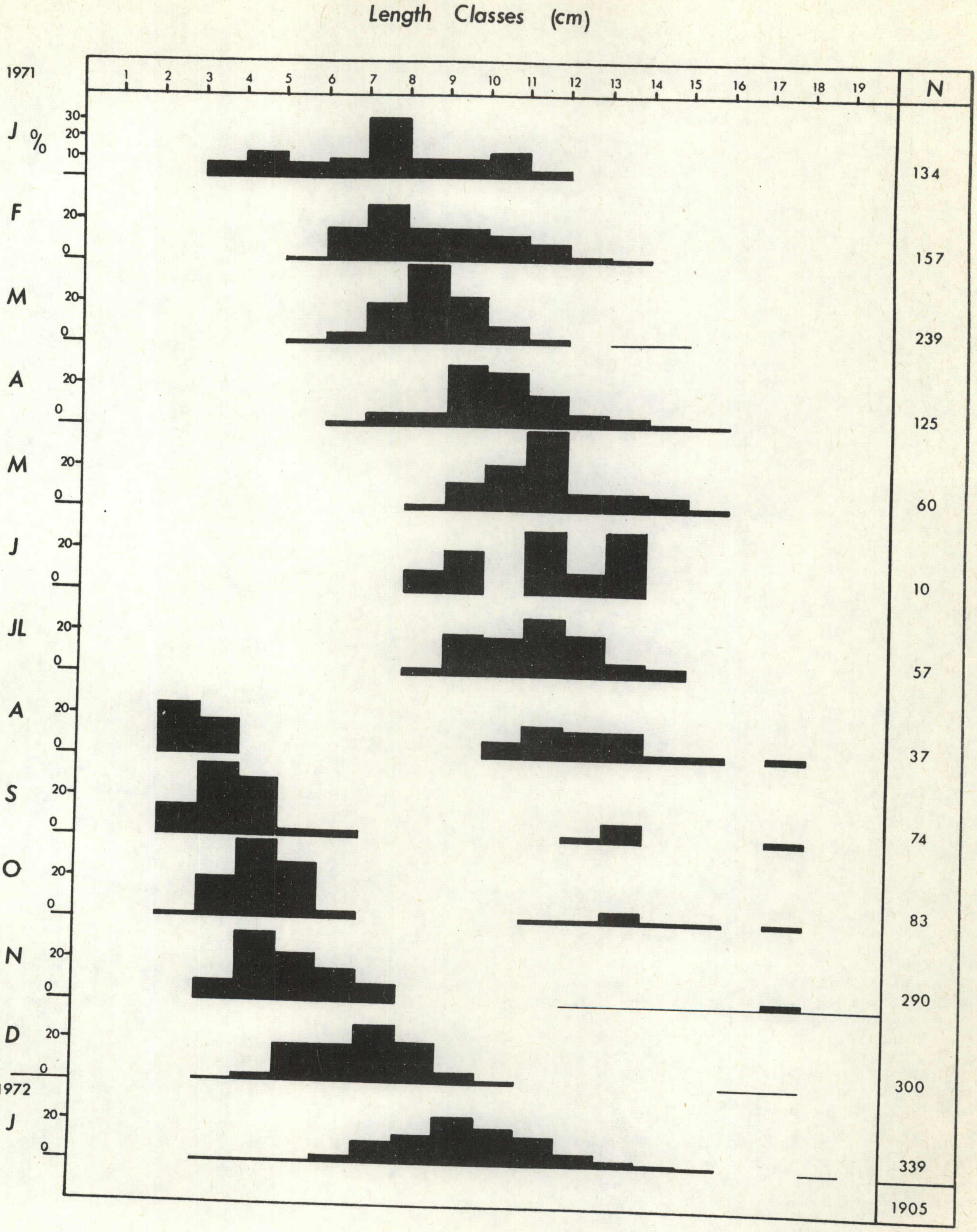


Figure 43. Percentage length composition of monthly catches of juvenile Rhabdosargus sarba (1971).

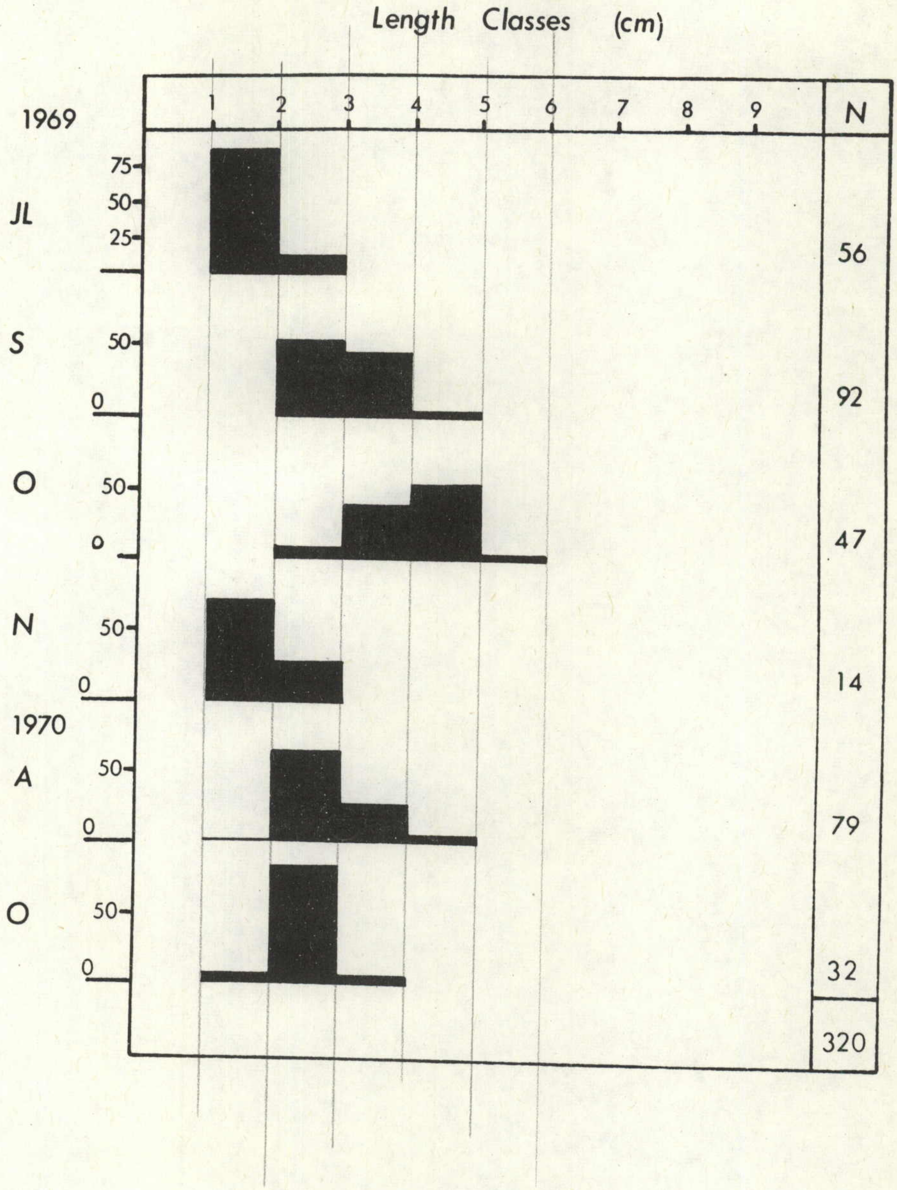


Figure 44. Percentage length composition of monthly catches of juvenile <u>Rhabdosargus holubi</u> (1969 and 1970)

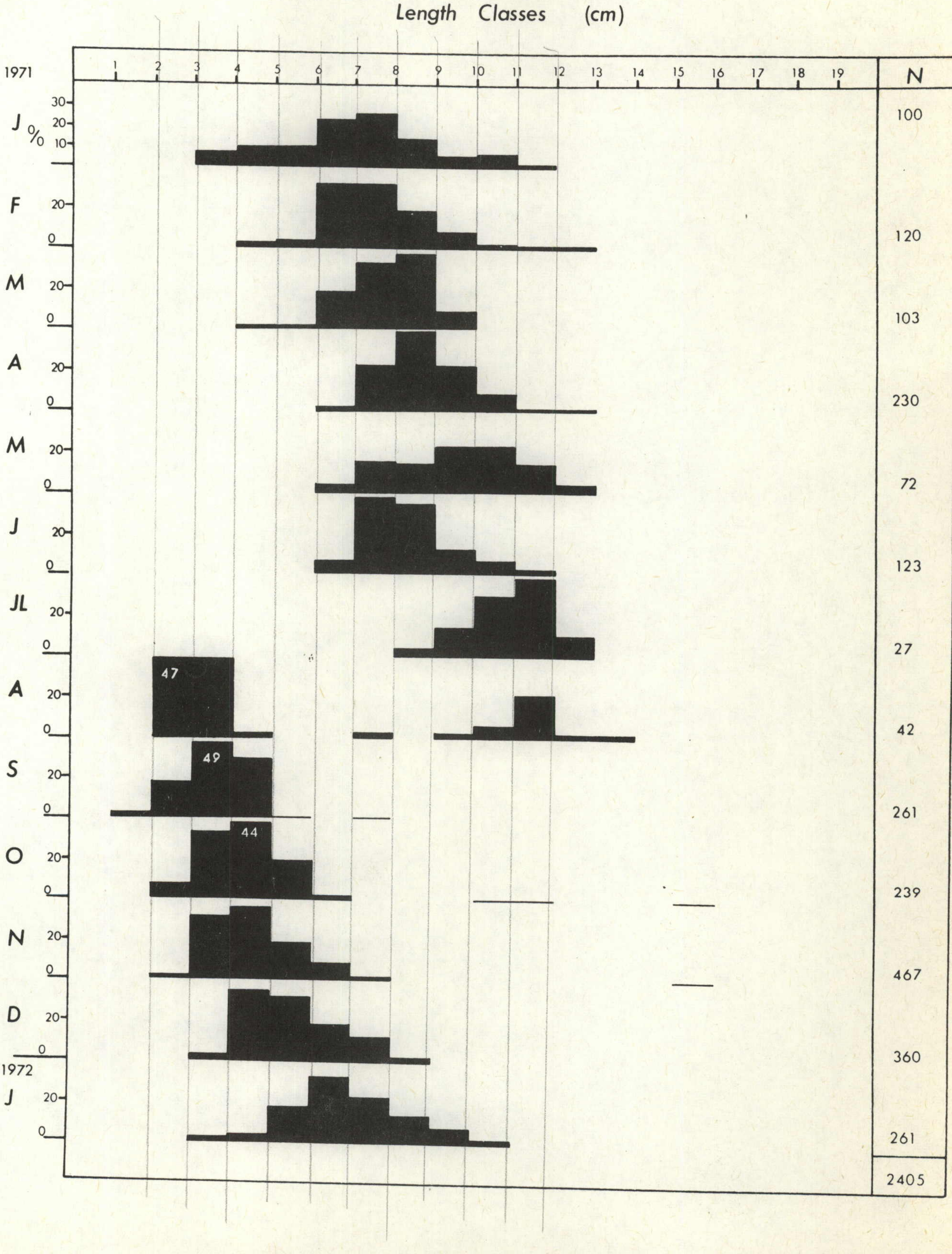


Figure 45. Percentage length composition of monthly catches of juvenile <u>Rhabdosargus holubi</u> (1971/72)

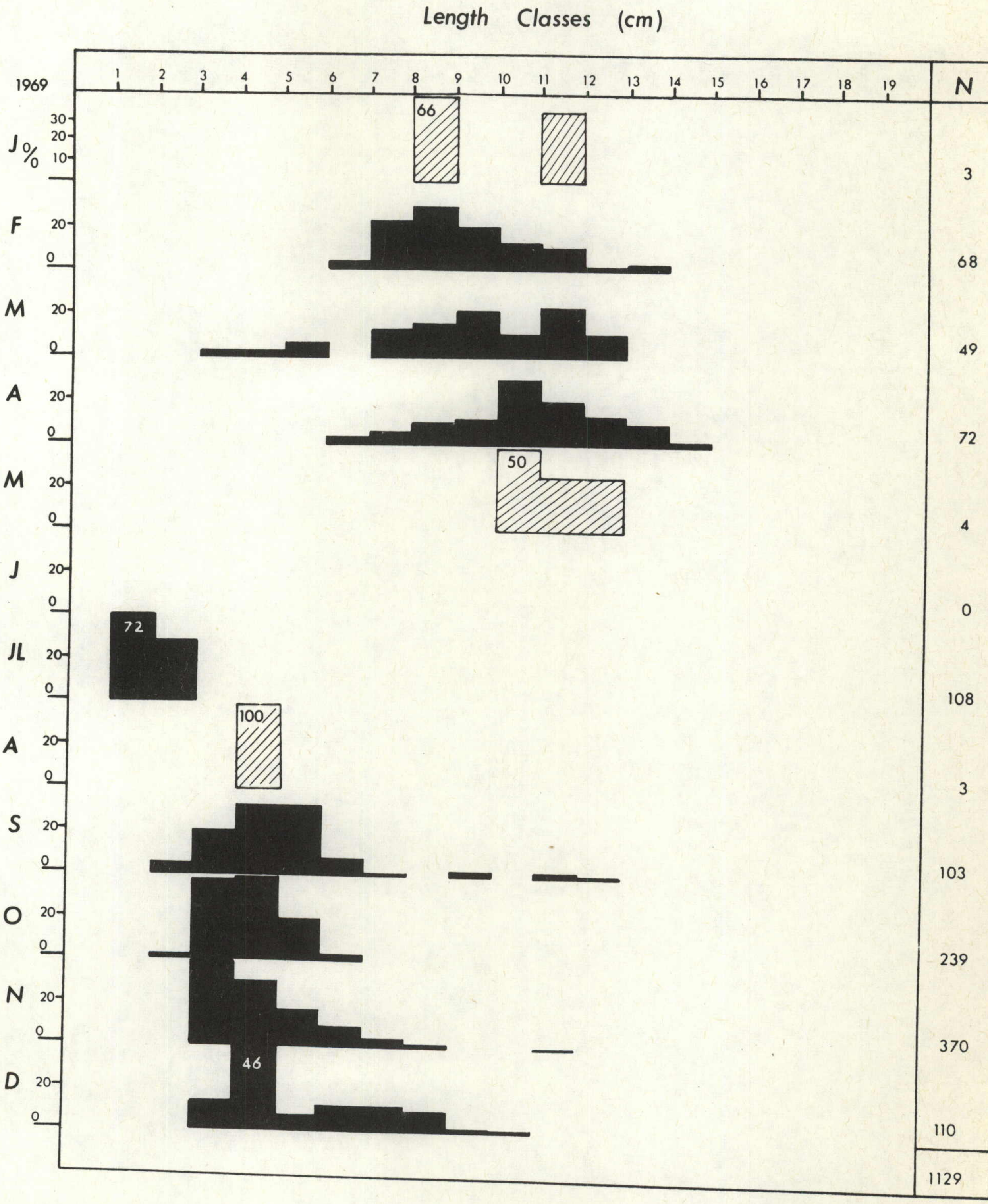


Figure 46. Percentage length composition of monthly catches of juvenile <u>Acanthopagrus berda</u> (1969).

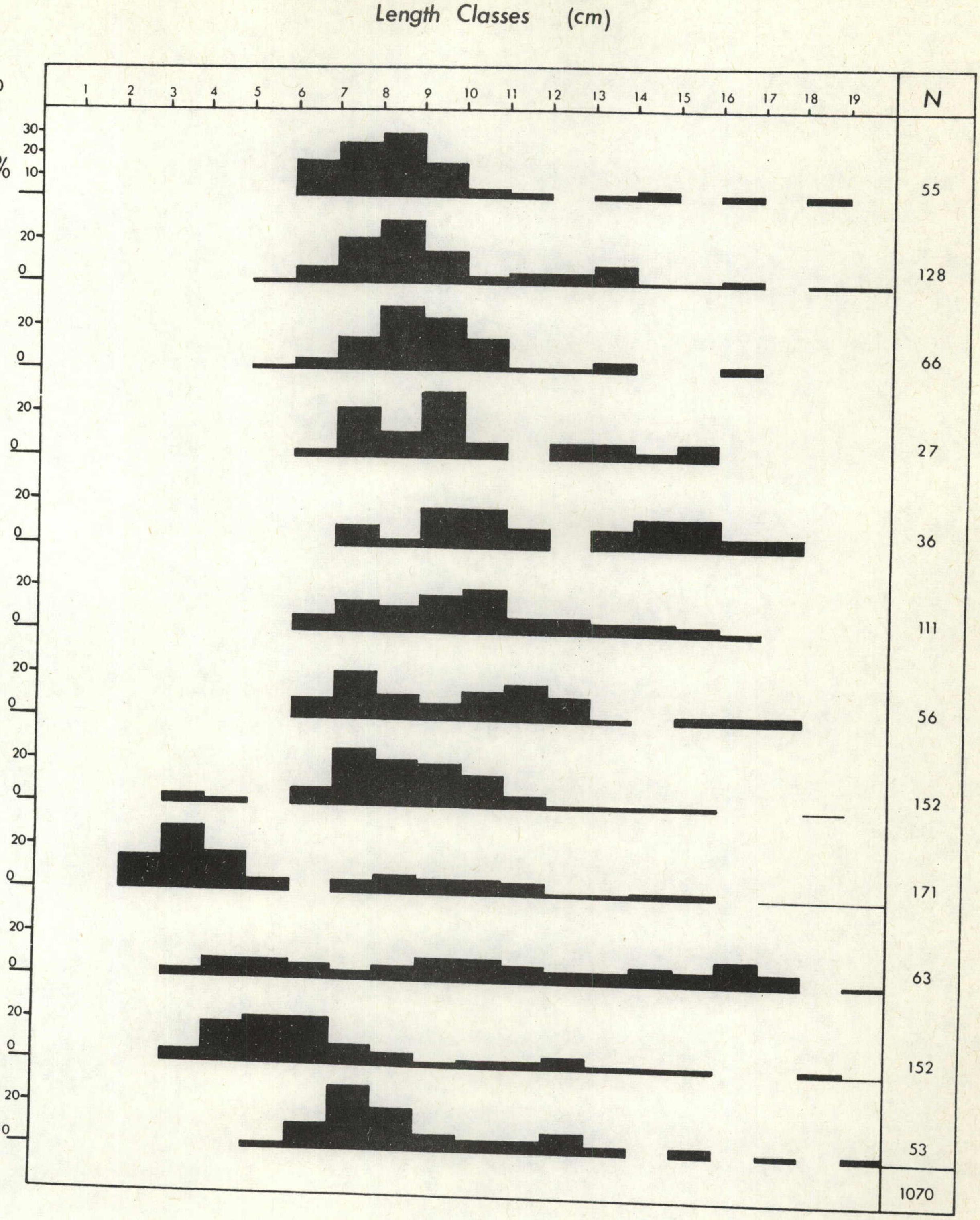


Table 47. Percentage length composition of monthly catches of juvenile <u>Acanthopagrus</u> <u>berda</u> (1970 and 1971 data lumped).

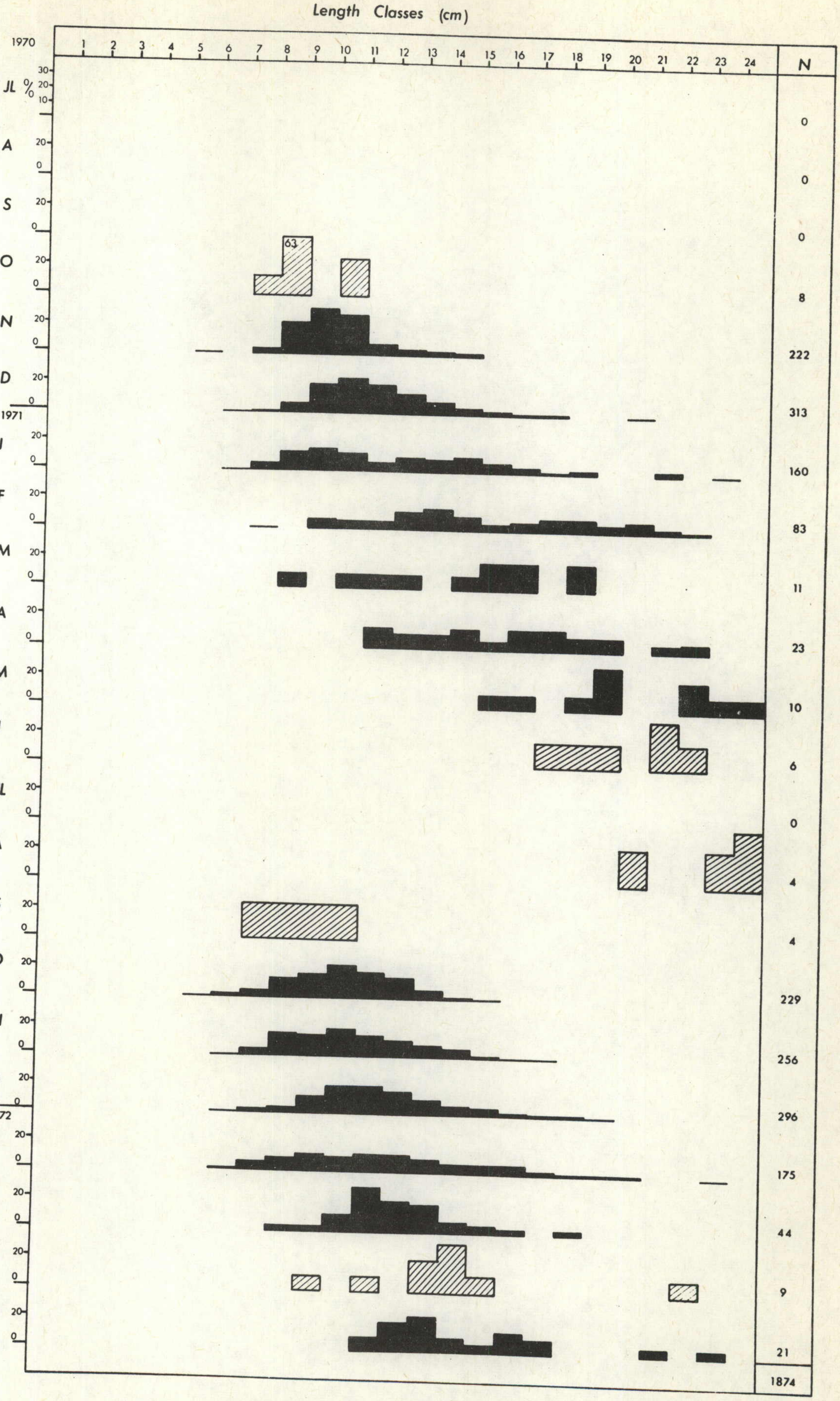


Figure 48. Percentage length composition of monthly catches of juvenile <u>Argyrosomus hololepidotus</u> (1970-1972)

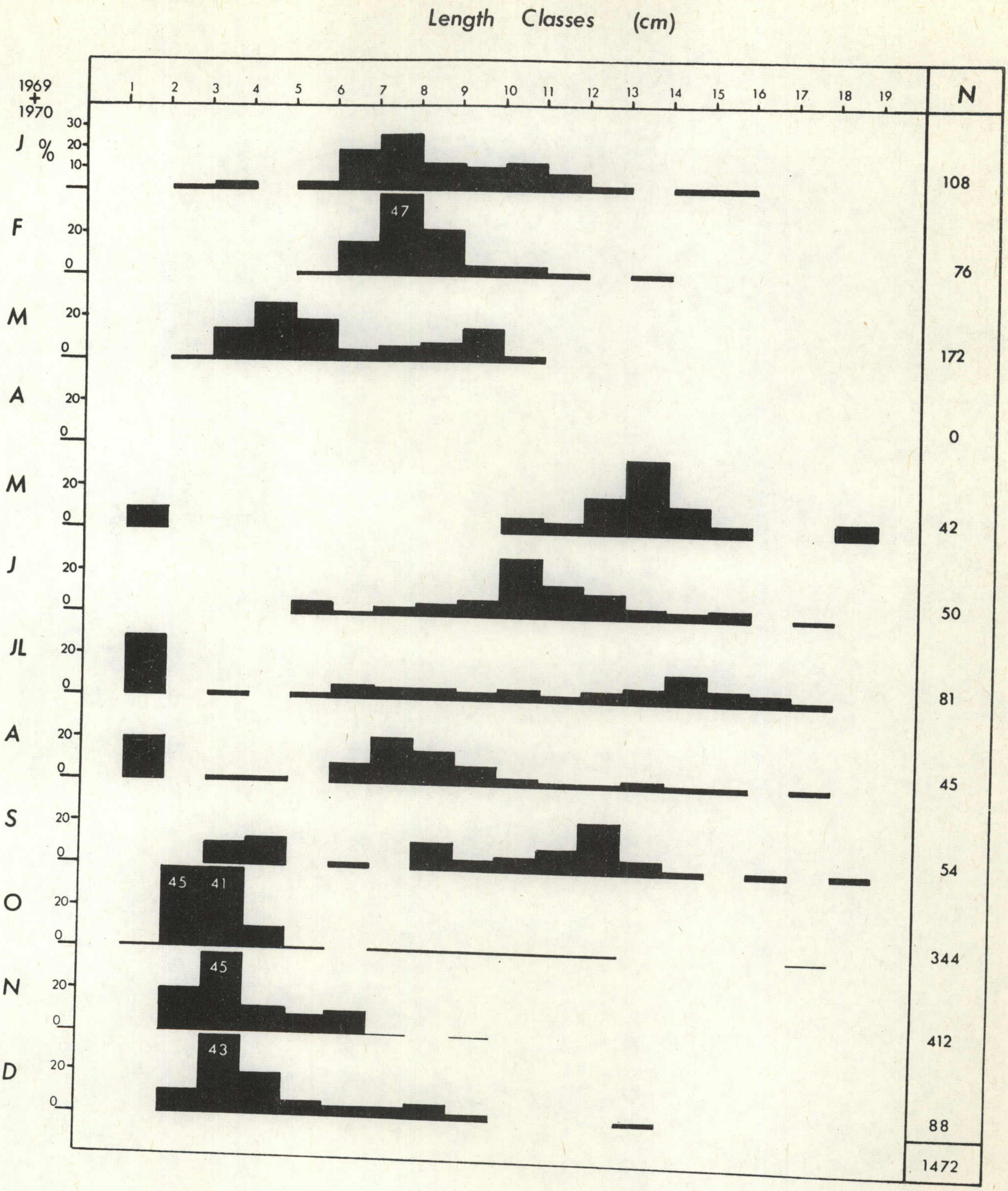


Figure 49. Percentage length composition of monthly catches of juvenile <u>Liza macrolepis</u> (1969 and 1970 data lumped).

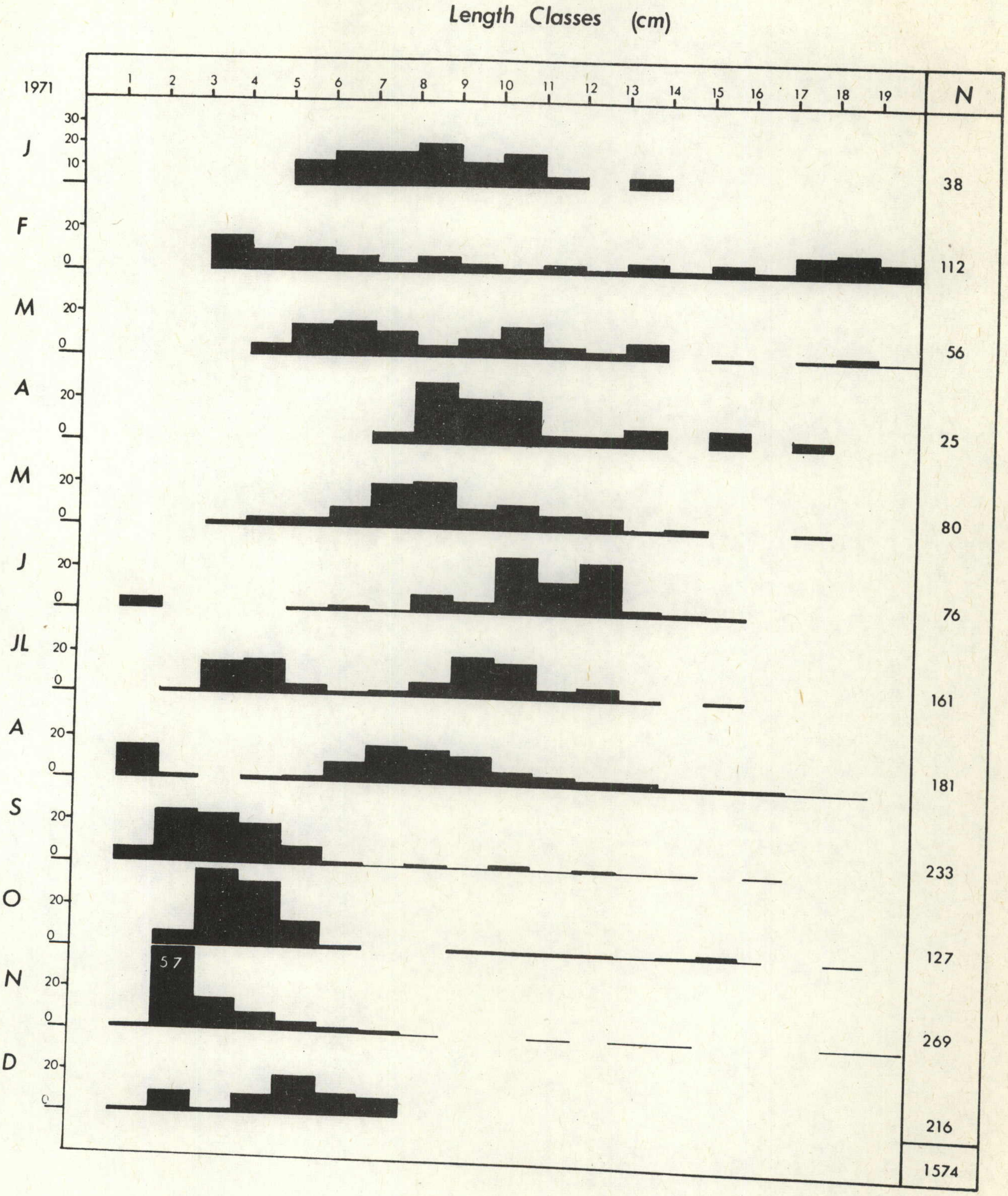


Figure 50. Percentage length composition of monthly catches of juvenile <u>Liza macrolepis</u> (1971).

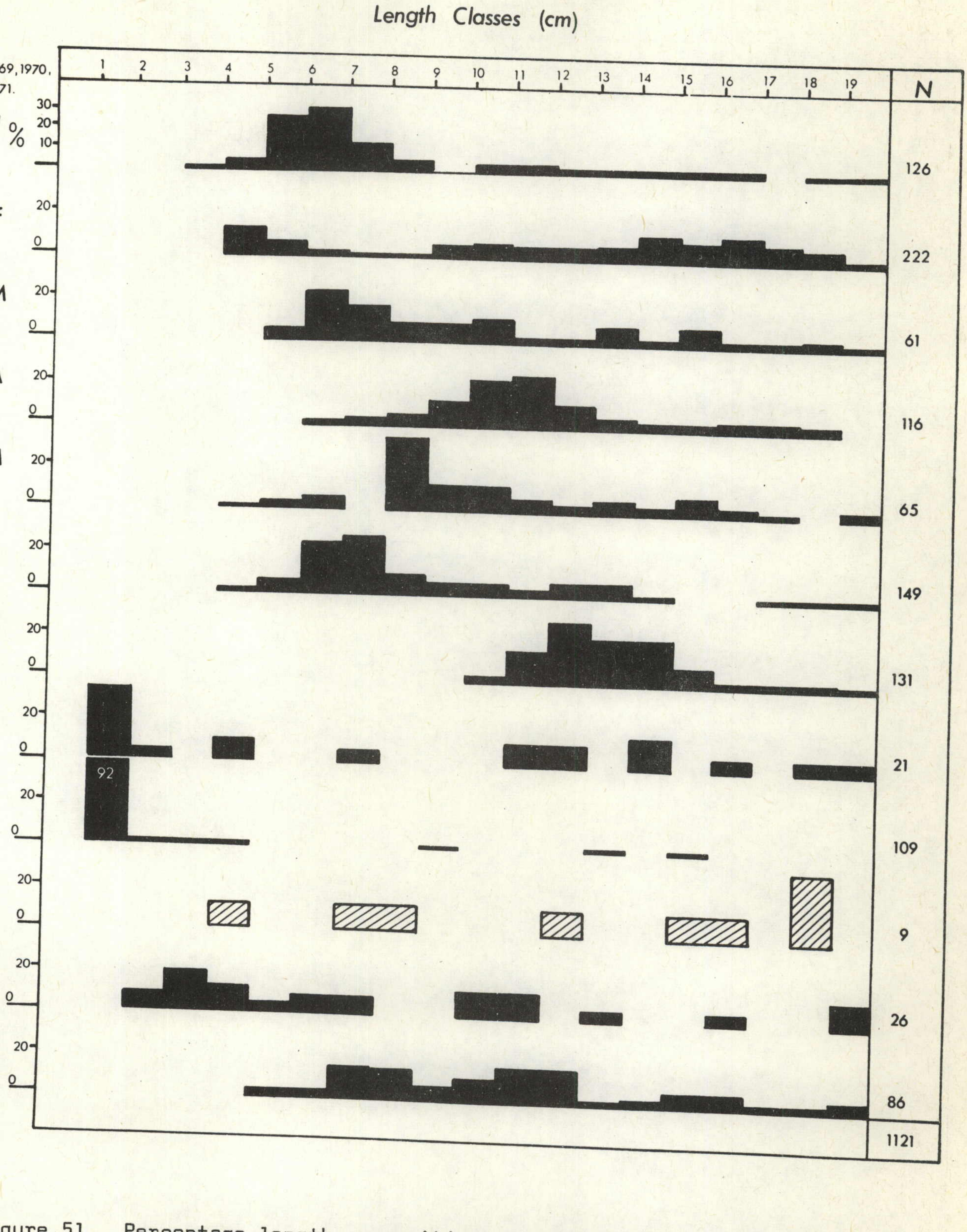


Figure 51. Percentage length composition of monthly catches of juvenile <u>Liza dumerili</u> (1969, 1970 and 1971 data lumped).

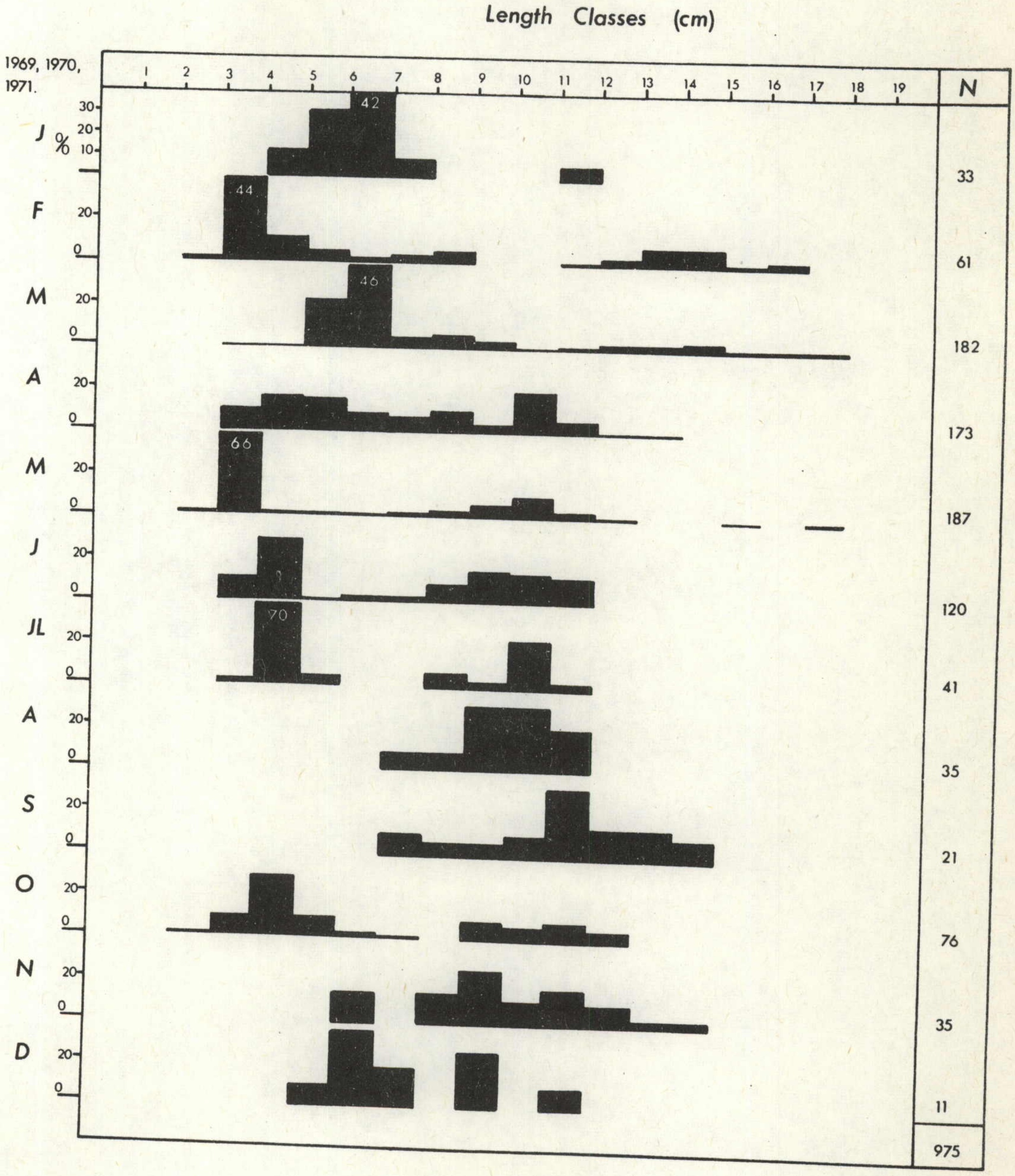


Figure 52. Percentage length composition of monthly catches of juvenile Valamugil buchanani (1969, 1970 and 1971 data lumped).

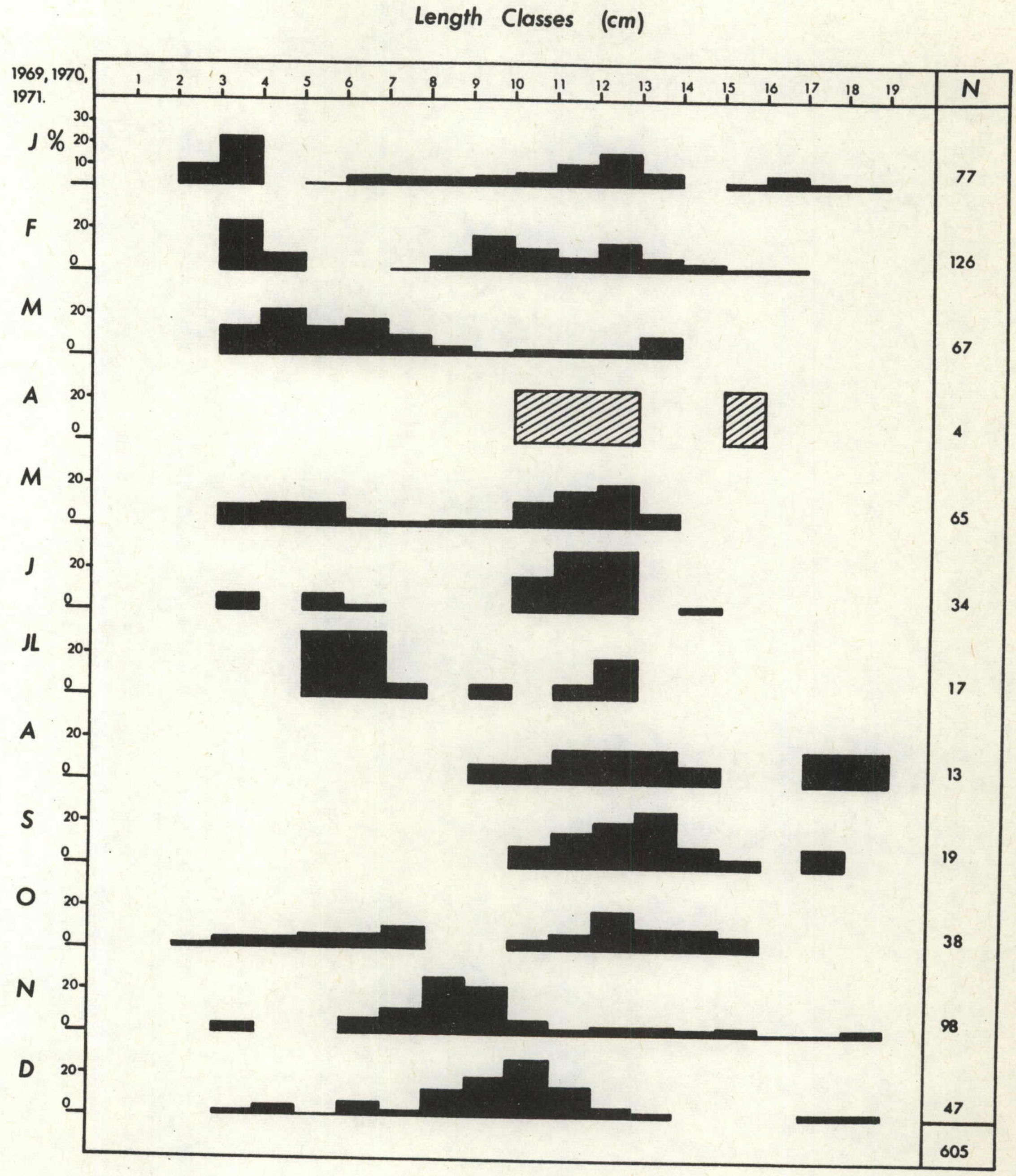


Figure 53. Percentage length composition of monthly catches of juvenile <u>Valamugil cunnesius</u> (1969, 1970 and 1971 data lumped).

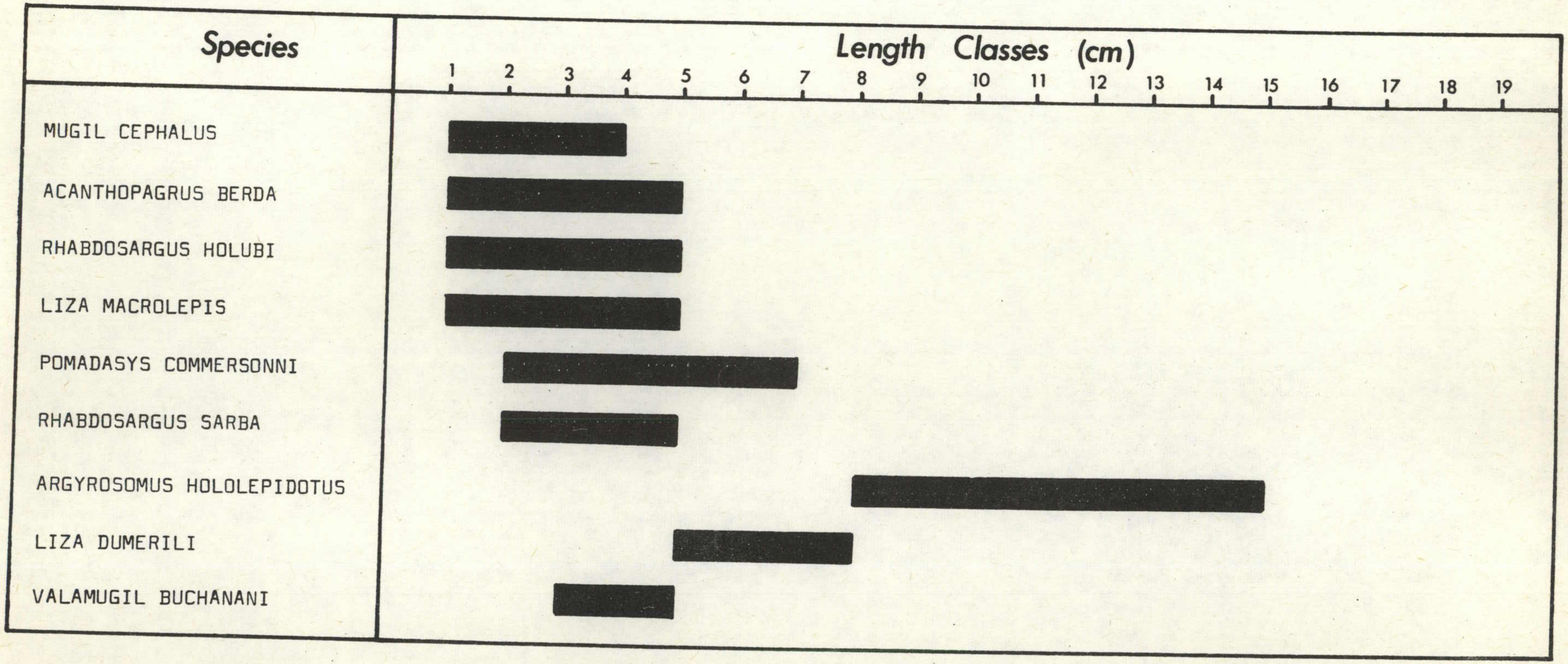


Figure 54. Length ranges of juveniles of the main species of estuarine fish of Natal during their most active phase of migration into estuaries.

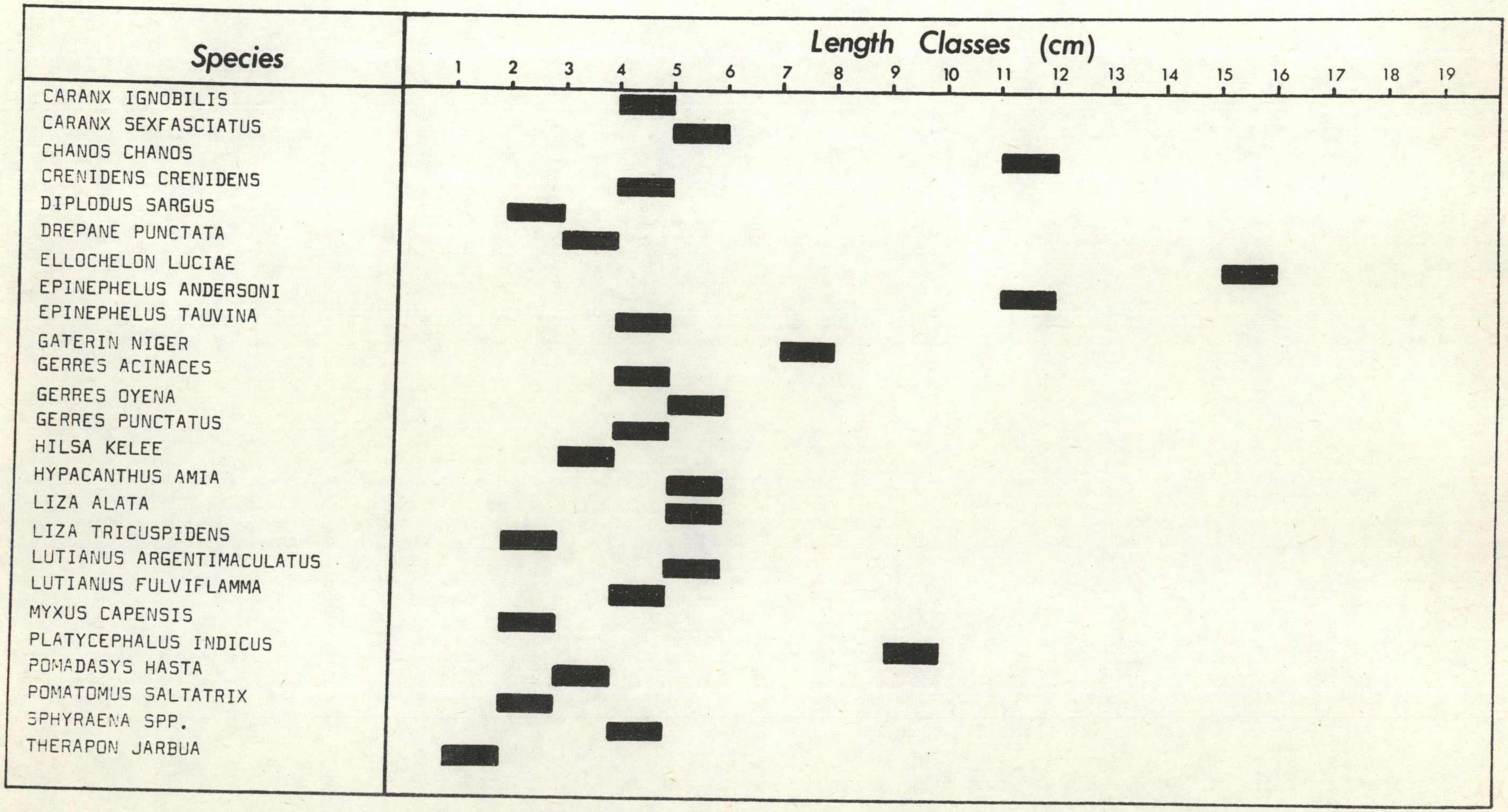
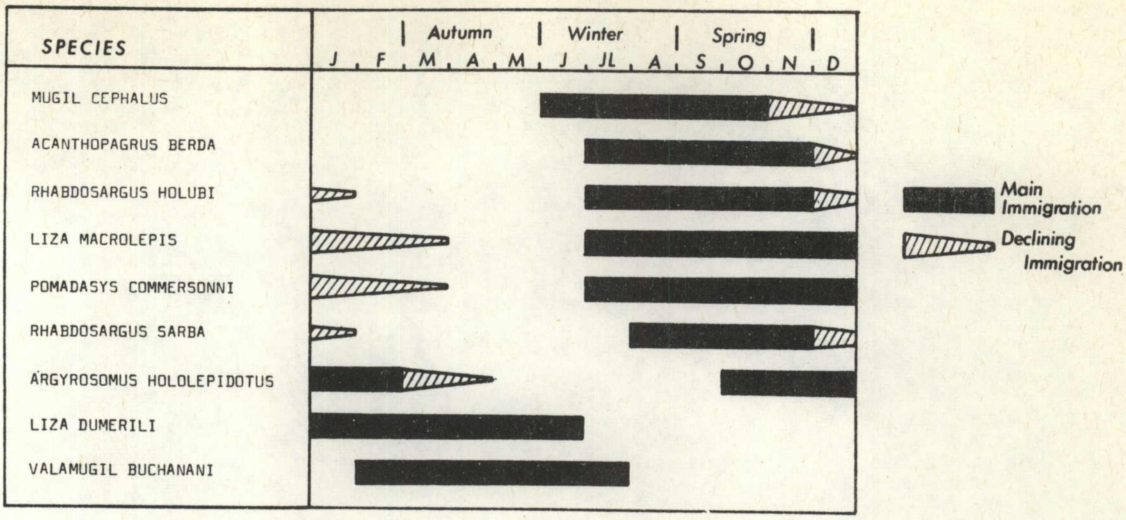
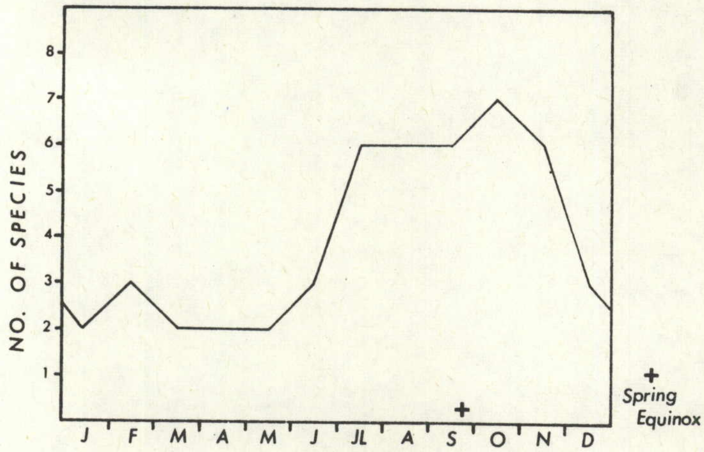


Figure 55. Lengths of juveniles of angling and food species when they first start migrating into Natal estuaries. (The more comprehensive data available for the main estuarine species are presented separately in Figure 54).

56a



b



c

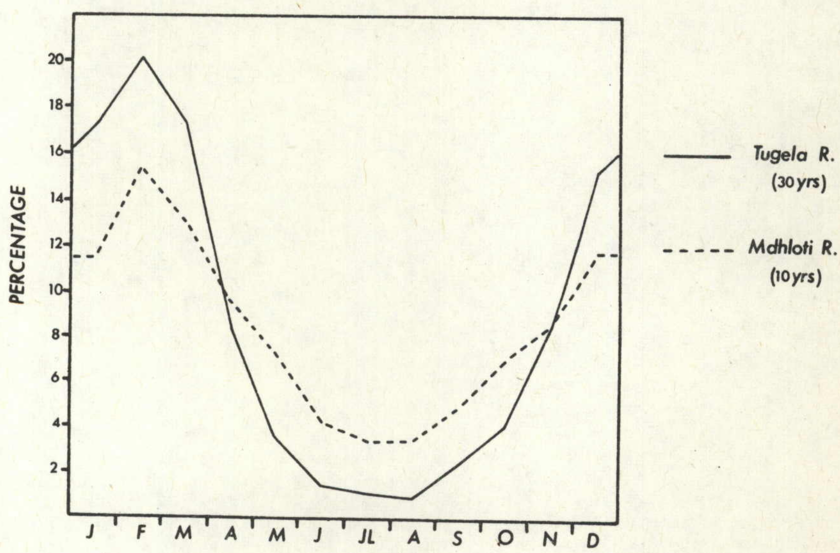


Figure 56a. Months of migration of juveniles into Natal estuaries.

Figure 56b. Monthly variation in the number of species migrating into Natal estuaries (the frequencies are derived from the main periods in Figure 56a).

Figure 56c. Mean monthly river flow expressed as a percentage of mean annual flow.

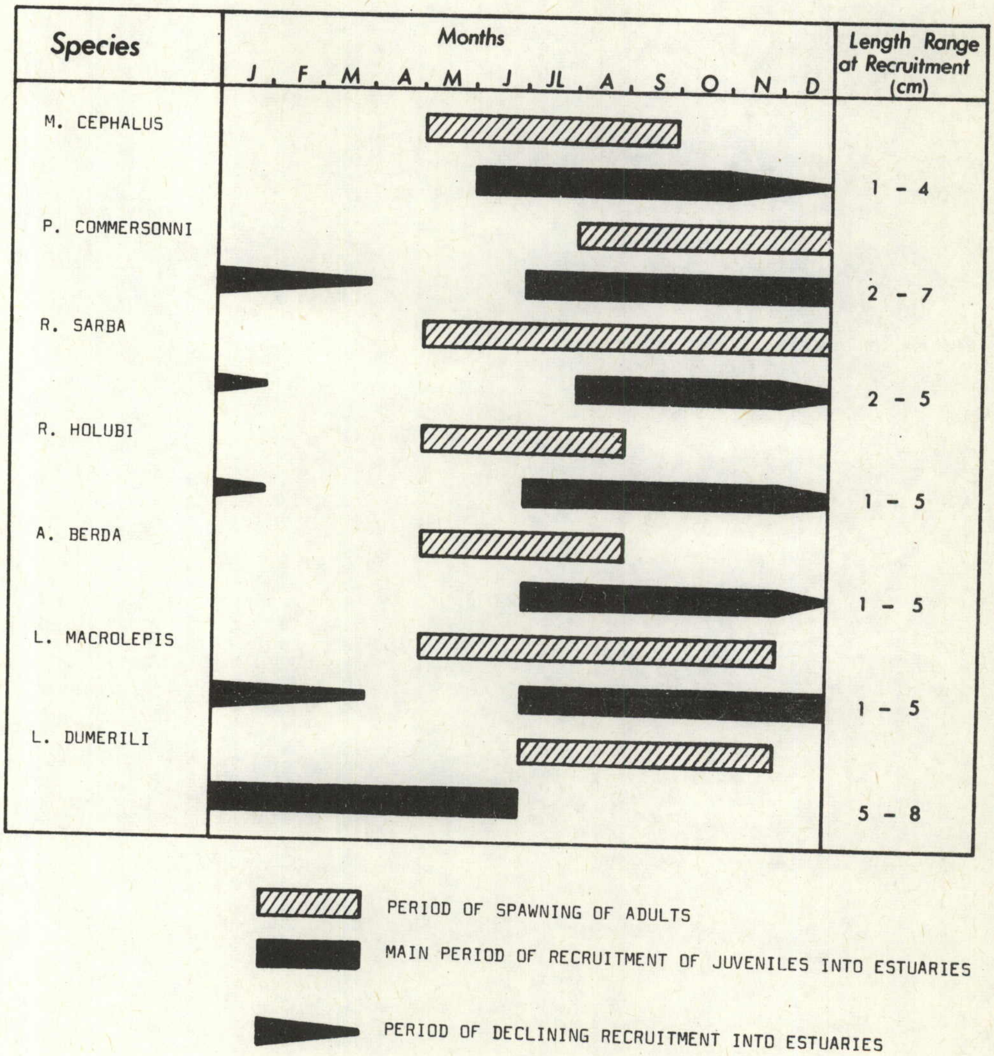


Figure 57. Relationship between the months of spawning of adults and periods of migration of juveniles into estuaries.

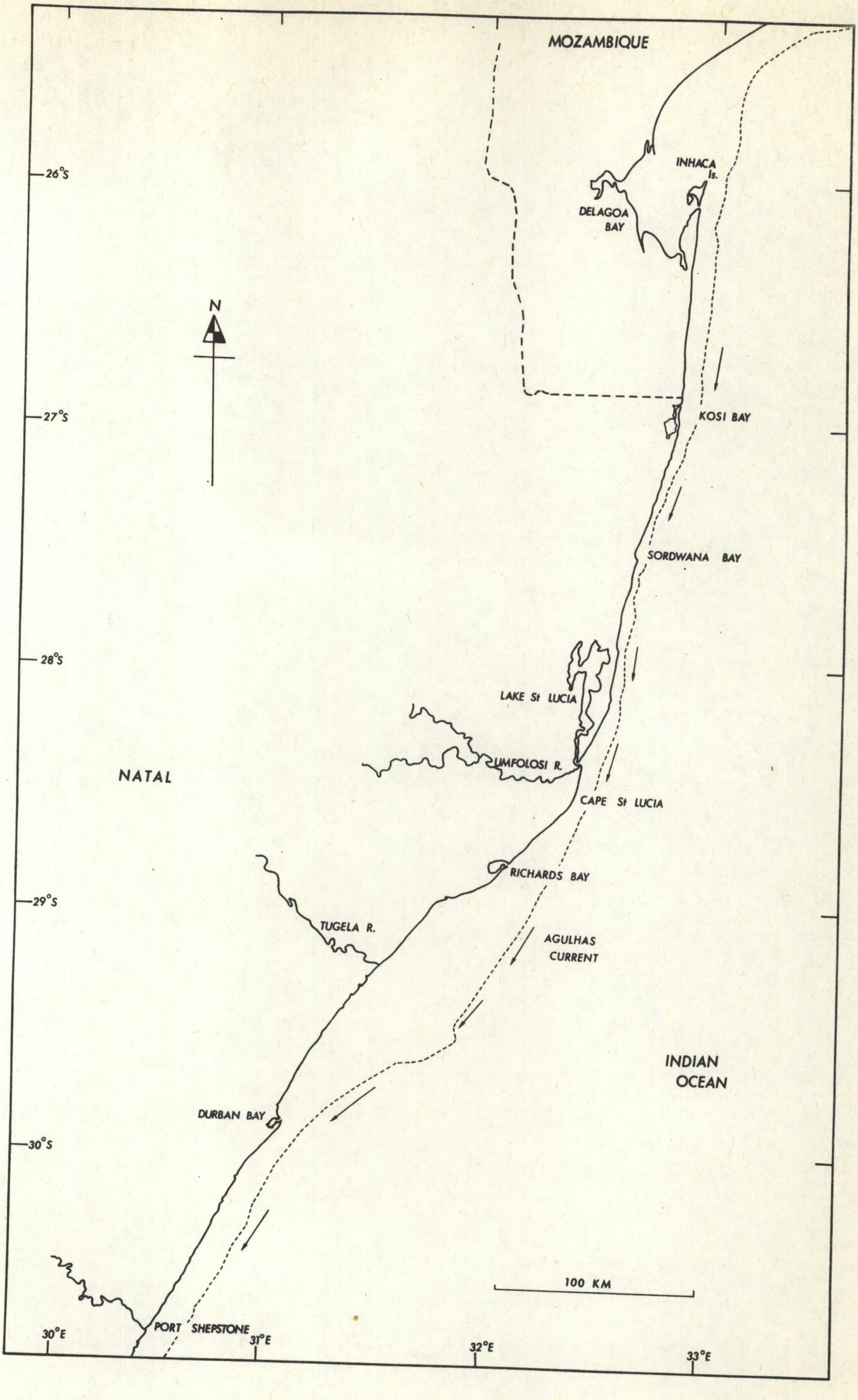


Figure 58. Map of Mozambique and Natal coasts between Inhaca Island and Port Shepstone. The 100 fathom depth contour is shown as a broken line and the Agulhas Current is arrowed.

ANNEXURE: A

ASPECTS OF THE BIOLOGY OF *MUGIL CEPHALUS* IN A HYPERSALINE ESTUARINE LAKE ON THE EAST COAST OF SOUTH AFRICA

John Henry Wallace

Paper presented at the International Symposium on the Aquaculture of Grey Mullet; held in Haifa, Israel, July 1974. Proceedings to be published in the journal 'Aquaculture' during 1975.

SUMMARY

The distribution of *Mugil cephalus* in a lake system with salinities ranging from 35‰ to more than 90‰ is described. Evidence is presented that the biology was not adversely affected by levels of 60 - 70‰ and that aquaculture under these conditions could have been successful.

Details of two annual seaward spawning migrations are reported in relation to the unusual hydrological and topographical features of the St. Lucia lake system. Possible mechanisms involved in seaward orientation are discussed and although the role of steep salinity gradients and gross salinity change is not discounted, it is suggested that organic cues derived from sea water inflow and fresh water drainage might also serve an orientation function.

Spawning has not been recorded in the system and the inability of this species to spawn under estuarine conditions is confirmed by examination of ripe specimens trapped by the closure of the estuary mouth.

INTRODUCTION

Mugil cephalus is the most important species of mullet in the estuaries of Natal and the Transkei (latitudes 26deg.50min.S to 32deg.40min.S). A study of its biology has formed part of a programme of research on the fishes that occur in the 86 estuaries of this 814km stretch of coast. The largest of these is the St. Lucia lake system (31 000ha) where the topography and high salinities that prevailed during 1969/1970 revealed some interesting aspects of the biology of this species. These are outlined as it seems unlikely that similar environmental conditions are duplicated in many other parts of the world.

St. Lucia (Fig.1) is a long (40km), narrow (3 - 8km, max. 21km) lake lying roughly parallel to the coast and connected to it by the Narrows, a winding channel 21km in length and about 100m wide. The lake is very shallow, having an average depth below mean sea level of 0,6 - 1,2m and a maximum depth of about 2m. Four rivers drain into it, their points of entry being in those parts of the system most remote from the sea. The small Mpate river flows into the northern Narrows. Evaporation exceeds rainfall and in dry years river inflow is so small that the lake drops below mean sea level. Consequently sea water flows into the system and continued evaporation during long periods of drought produces a reversed salinity gradient (Day *et al*, 1954; Kriel, 1966; Millard and Broekhuysen, 1970).

METHODS

Regular monthly gill netting with four different mesh sizes was conducted in the lake and Narrows during 1969 and 1970. Juvenile sampling was undertaken with a variety of netting gear. Procedures well established in the literature were adopted for investigating reproductive state and other biological parameters. Movements of mullet shoals were indicated by net catches and by visual observations from patrol boats - in the very shallow water concentrations of mullet are easily visible when they are disturbed. Salinities were taken by the temperature-corrected hydrometer technique. Length was measured as the maximum distance from the snout to the tip of the upper caudal rotated ventrally to the mid-line.

RESULTS

Adaptation to hypersalinity

The salinities recorded at sampling stations representative of the different regions of the lake are set out in Figure 2, from which it is apparent that the whole lake became increasingly hypersaline from mid-1967 to mid-1970. The north lake always experienced higher salt concentrations than the south and levels in excess of 90°/₀₀ were recorded over a wide area.

Despite these conditions the lake supported an extremely rich mullet population with a length range of 18 - 680mm. Surprisingly this species favoured the high salinity area north of Fanies Island (Fig.1) and was only abundant in the south during the period of inward migration of juveniles and seaward migration of pre-spawning adults. The interim years were spent in the north where a continuous length range was recorded.

Small juveniles less than 27mm in length were sampled at salinities of up to 50°/₀₀, while a group of specimens of 45 - 57mm was recorded in 78°/₀₀. Two dead adults were found floating on the surface at 75°/₀₀ and 78°/₀₀, but the capture of live adults at 86°/₀₀ suggests that these corpses might have drifted away from where death actually occurred. In general, gill net catches and sightings indicated that *M. cephalus* from about 100mm upwards was very abundant at salinities between 60 - 70°/₀₀, but tended to avoid higher salt concentrations.

Available evidence suggests that the high salinities did not adversely affect the biology of the species. Adult specimens in pre-spawning condition in the north lake had mean condition factors ($K = {}^{W}/0.01L^3$ as used by Thomson, 1951) of 1.1 - 1.2. These compare favourably with Thomson's data for Shark Bay, Western Australia and with the upper end of the range for sample means reported by Kestevan (1942). There is therefore no sign of undernourishment in St. Lucia mullet, which accords with observations in the field that they fed actively, were healthy and fat in appearance and extremely vigorous as evidenced by their jumping behaviour. Mullet with developing gonads were netted in salinities as high as 70°/oo and gonad weights of 230 - 560gm were recorded for females 500 - 650mm in length which were migrating seawards through the south lake at salinities of 50°/oo.

Spawning migrations

(i) 1969

During the summer months mullet shoaling intensified in the north lake as a prelude to the annual migration to sea to spawn. This pattern is evident from the catches taken in the south (Fig.3) which show that mullet were absent during the period October 1968 to February 1969, but suddenly appeared in March. Under the conditions prevalent at that time this southward movement involved a reduction in salinity from about 70°/oo to 35°/oo (Fig.2). Continued migration through the Narrows and out to sea seemed imminent but did not take place. During late March and early April very heavy rains reduced the salinity in the south to less than that of the sea (Charters Creek 23°/oo) and in the northern Narrows where the Mpate river was in flood, down to fresh water for a short time. In the north salinities dropped to 40 - 50°/oo.

Gill netting in the south during the first half of April revealed that the shoals were no longer in the area and this was supported by the lack of sightings. Large shoals were however located north of Fanies Island where salinities were approximately the same as they had been in the south before the rains and there is little doubt that they had moved there from the south lake. Towards the end of April and early in May mullet numbers increased in the south where salinities had risen to 28 - 32°/₀₀. During June the species was again abundant, salinity levels of 35 - 38°/₀₀ were recorded and mullet were moving out to sea. By July most of the migrants had passed through the south lake and thereafter the species was virtually absent from the area.

(ii) <u>1970</u>

From the map of St. Lucia it can be seen that the entrance to the Narrows consists of the wide Brodies Crossing area and the very much narrower Potters Channel. Both are very shallow but during the 1969 migration the lake was slightly above mean sea level (M.S.L.) and both routes were used. In 1970 lake levels were between 30 - 40cm below M.S.L. and traverses of the Brodies area showed that its northern entrance was only 8 - 13cm in depth and the gap south east of Mitchell Island was even shallower. Thus with the exception of the few occasions when north easterly winds increased the water depth to 20cm, this route could not be utilised by the thousands of migrating mullet. The only alternative was through the gap west of Mitchell Island and into Potters Channel. Despite the fact that there was a discharge of sea water into the lake via this route it was uncertain whether the shoals would locate and then venture through it as the entrance was only 30m wide and 30 - 45cm deep.

Mullet arrived in the south lake in February (Fig.3), but netting and sightings showed that their abundance dropped off in March and that they had retreated northwards for about 10km. By April they had returned to the south causing an increase in catch rates, which reached a maximum in May. Early in May mullet were first observed moving seawards through Potters Channel and under the shallow conditions prevailing at that particular time, the Brodies route was not being utilised. Continued migration seawards was responsible for the reduction in abundance in the lake during the ensuing months. (The high catch rate in September and hence departure from the cycle established in 1969 is an unusual event associated with the closure of the estuary mouth).

Spawning and the closure of St. Lucia estuary during the 1970 migration

Despite examination of thousands of M. cephalus during the spawning season, only one 'ripe running' female has been been recorded in the St. Lucia system and this was taken in clear water on an incoming tide within 150m of the estuary mouth. Spawning is therefore not considered to occur in the lake or in the turbid water of the Narrows.

Confirmation of the lack of spawning under estuarine conditions was provided in 1970 when the estuary mouth closed at the peak of the seaward migration and isolated many ripe specimens from the sea. For about two weeks salinities remained at 35°/oo but then dropped to 20 - 28°/oo for the next three months. No spawning was detected and histological examination confirmed macroscopic observations that ova were breaking down and the contents being resorbed. This evidence supports the statement of Abraham (1963) that M. cephalus is unable to spawn except in sea water.

The circumstances of capture of the single 'ripe running' female and the abundance of immediately pre- and post-spawning mullet in the estuary, suggests that spawning takes place locally. It seems likely that it occurs off the sandy beaches and on the continental shelf as very large concentrations of fish occur in these areas at this time of the year. However the continental shelf is only 5km wide in this region and the strong Agulhas current flows south westwards along its outer edge (Oliff, 1969). Thus the spawning area may be relatively small and southward distribution of larvae along the South African East Coast can be expected.

DISCUSSION AND CONCLUSIONS

When normal hyposaline estuarine conditions occur in St. Lucia lake M. cephalus is fairly evenly distributed throughout the system. Thus the preference shown for the north lake when it was strongly hypersaline suggests that this area must have had some particular attraction for the species. The most likely explanation is that a salinity-induced imbalance in the benthos occurred due to differences in tolerance levels and that there was a 'bloom' of some favoured food organism. Whatever the reason, the fact that a wild population flourished under these conditions indicates that aquaculture of M. cephalus might also be successful in hypersaline areas.

An investigation of the factors involved in the seaward orientation of St. Lucia mullet is beyond the scope of the project being undertaken but in view of the unusual environmental conditions and the details that have been recorded, some attempt at interpreting the results is called for.

It is difficult to discount the possibility that the steep north/south salinity gradient in St. Lucia helped the mullet shoals to orientate in a general seaward direction. It also seems likely that a gross salinity change, such as a 'plug' of fresh water in the Narrows, could have a disruptive effect on migration. However the resumption of the seaward migration from hypersaline water into the south lake (late April 1969), when its salinity had risen to only 28$^{0}/_{00}$, is difficult to explain on the basis of salinity gradients alone and tends to implicate some additional orientation mechanism.

Research by Creutzberg (1961) on the location of inland waters by elvers reveals their apparent indifference to salinity and the occurrence of an attractive substance in the inland water, the nature of which was unknown but was thought to be odorous and was shown to lose its attractive potency with time. Kristensen (1963) carried out experiments to determine what attracted mullet fry to hypersaline bay water in preference to sea water and concluded that organic compounds formed the attractive component. The extremely sensitive olfactory sense of young eels was demonstrated by Teichmann (as quoted by Creutzberg, 1961) who found that they were able to detect a β-phenyl-ethyl alcohol dilution amounting to one or two molecules in the nasal capsule. Similar sensitivities may well apply to anadromous fishes such as salmonids for which Nordeng (1971) and Solomon (1973) provide evidence that the homing ability is influenced by the production of pheromones by the fish population already in their home waters.

In the case of mullet moving into estuarine and brackish areas, such precise navigation is probably not necessary and a positive response to an organic substance typical of inland water in general would seem adequate. In the converse situation, some seaward orientation mechanism is necessary and although this could perhaps be a negative response to the same compound, the complex nature of sea water raises the possibility of the utilisation of a different organic cue which is typical of the marine environment.

Support for the existence of a marine cue is provided by the St. Lucia situation in which inflow of sea water into the southern lake during the 1969 drought could have served to maintain a seaward orientation gradient, but where a negative response to inland water would have failed to do so because there was no river inflow into the lake. If decomposition of the marine attractant occurred, as was reported for the cue for elvers, it would have prevented it from becoming concentrated towards the north and would have maintained a positive gradient towards the point of entry of sea water. Under non-drought conditions when the lake is at or above M.S.L. and the rivers (all of which enter the north lake) are draining into it, a negative response to some fresh water cue might orientate the fish seawards. Thus, depending on circumstances, mullet migrating from brackish water towards the sea might follow a decreasing concentration of an inland water cue or an increasing concentration of a marine cue.

Although speculative, this interpretation seems to hold some promise and in addition to the above general application to orientation in St. Lucia, provides the means of explaining the temporary retreat of mullet shoals towards the north lake during April 1969 (Fig.3). During the preceding months sea water was flowing into the lake and mullet could have moved southwards by the method already suggested. Exceptionally heavy localised rains in late March and early April raised lake levels by direct precipitation on the lake surface and by inflow of water from its immediate environs, particularly the Mpate river which was in flood for a short period. The former would merely have diluted the lake water and any attractive substance therein, but the latter was derived from an area of mixed forest and grassland and would have introduced organic compounds of terrestrial and riverine origin into the northern Narrows and southern end of the lake. This could be expected to produce a confusing situation if the migrants had been orienting on a marine cue. With the increase in lake level above M.S.L. and therefore cessation of further sea water inflow, a complete disruption of the migration would not be unexpected. Presumably the mullet's presence in water of recent terrestrial origin would have been contradictory to their biological urge to reach the sea to spawn and the retreat northwards could have been an avoidance reaction. Their reappearance in the south in May and June was associated with strong outflow from the system which would have displaced any 'offending terrestrial water' and facilitated movement out to sea with the lake water.

In March 1970 the unexpected reduction in mullet numbers in the south lake (Fig.3) was not associated with any interruption in the inflow of sea water through the Narrows. Insight into possible reasons for this arises from the experimental work of Collins (1952) who gives a convincing explanation of the role of movement in providing a comparison of intensities of stimulation at different points that are successive in time and therefore in distance. This makes it possible for fish to become oriented in much weaker gradients than would be possible if orientation was dependent on instantaneous perception of changes in stimulation. The northward movement of mullet might therefore have been an attempt to set up detectable differences in concentration of the marine cue so that the direction of its gradient could be determined and then followed.

Surprisingly, in the 14 years which elapsed between the publication of Talbot's paper and the start of the present programme, no new detailed study of the life history of an estuarine fish species was undertaken. A review of the state of knowledge of the biology of estuarine fishes at the start of the present programme has therefore to be based on the literature already quoted above. This reveals that the basic pattern of utilisation of estuaries by fishes was understood in its broadest terms. Breeding was considered to take place at sea, with adult fish moving into estuaries to feed. Juveniles were known to be abundant in the estuarine environment which served a nursery function by providing rich feeding grounds (particularly in areas with prolific aquatic vegetation), as well as protection from predators. A start had been made in the study of feeding habits within certain estuaries and estimates of size at sexual maturity and breeding season had been made for some of the species of major importance (more detailed reference will be made to these data in the relevant sections of this thesis). However it was only in the case of R. globiceps that comprehensive data on growth rate, ageing, feeding, length frequency composition and size at maturity were available, and for which sampling in the estuarine and marine environments had proved conclusively that spawning occurred at sea and that only the juvenile phase was represented in estuaries.

Thus at the start of the present programme broad guidelines to the biology of estuarine fish were available in the literature. However there was a great need for factual documentation of biological events for which little or no evidence was available and for a detailed exploration of the biology and ecology of the estuarine teleost fauna of Natal in both its estuarine and marine phases.

3.2 Outline of sampling programme

Due to the wide scope of the programme it was necessary to divide it into the following phases:

Feasibility study: August to December 1968
Biology of adult fish in estuarine environment: 1969 and 197
Biology of juvenile fish in estuarine environment: 1971
Biology of adult fish in marine environment: 1972
Aspects arising from previous phases, including the geographic distribution of juveniles in estuaries: 1973

At the outset it was intended to concentrate most research effort on the St. Lucia Lake system as this is Natal's largest and richest estuarine area and is, furthermore, administered as a wildlife sanctuary. Thus it would be possible to apply the results more directly for purposes of conservation than in other estuarine systems which fulfil multiple functions. It was considered reasonable to suppose that the results obtained at St. Lucia would be generally applicable to estuarine fish in Natal, so diversification of the programme to include intensive sampling in other estuaries was not envisaged. However, during early 1969 the St. Lucia system showed signs of becoming hypersaline and because it seemed possible that aspects of the biology of the fish might be influenced by these conditions, the programme was extended to include Richards Bay (from May 1969) and Durban Bay (from September 1969). This permitted results generally representative of the biology of estuarine fish of Natal to be obtained.

3.3 Areas of sampling

It is considered unnecessary to give detailed descriptions of the three estuarine systems where research was undertaken because this would be repetitive of the published work of Day and Morgans (1956), Millard and Harrison (1952) and Day, Millard and Broekhuysen (1954) on Durban Bay, Richards Bay and St. Lucia respectively. For purposes of acquainting the reader with these areas a brief outline of each should suffice, but mention will be made of any significant changes which have taken place subsequent to the above publications.

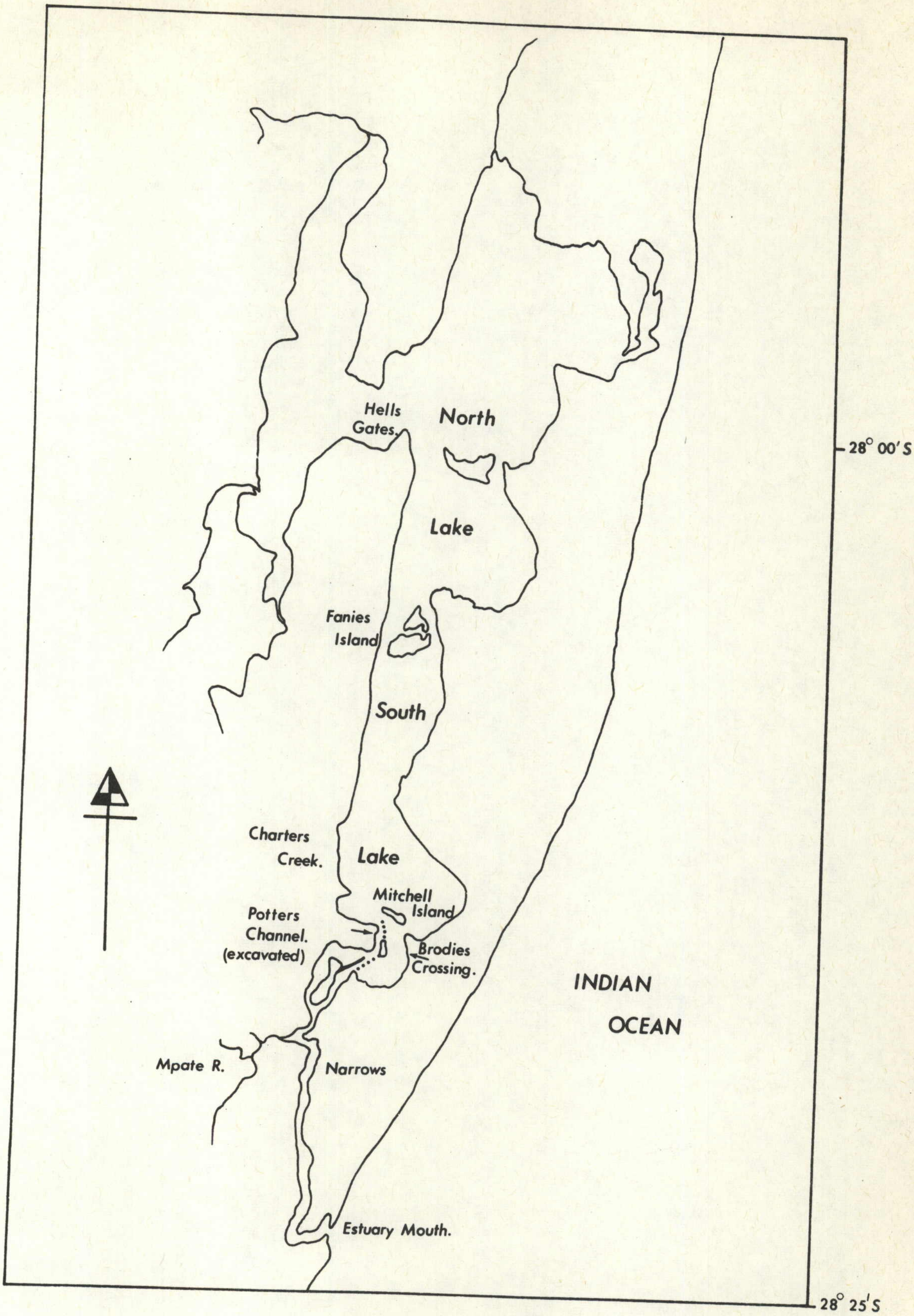
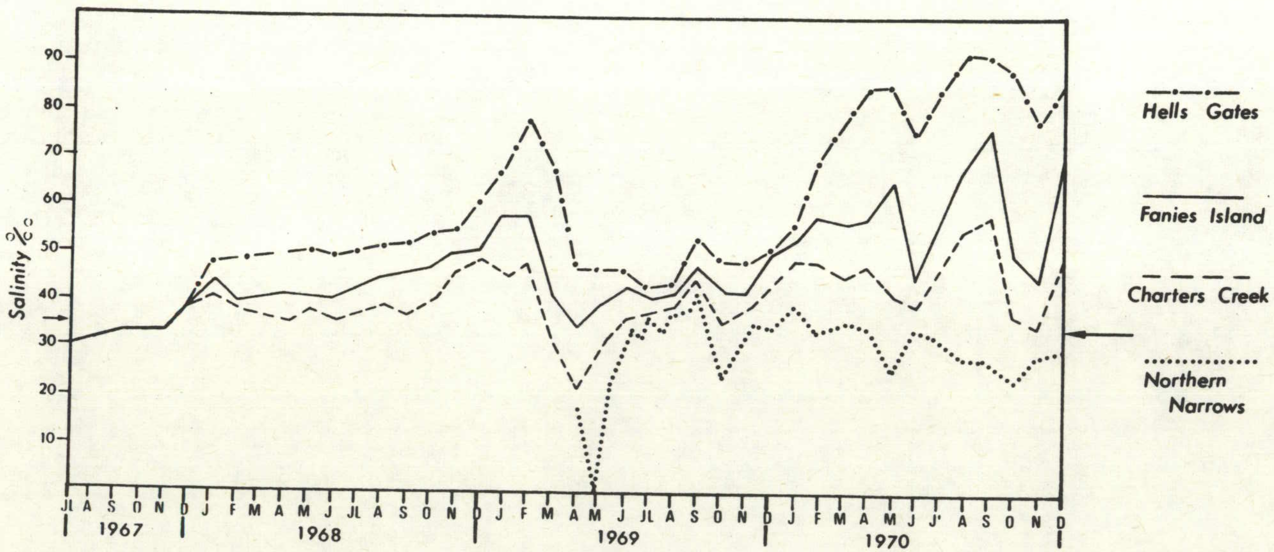


FIG. 1 THE St LUCIA LAKE SYSTEM

FIG. 2 SALINITY REGIME IN St LUCIA LAKE 1967 - 1970.



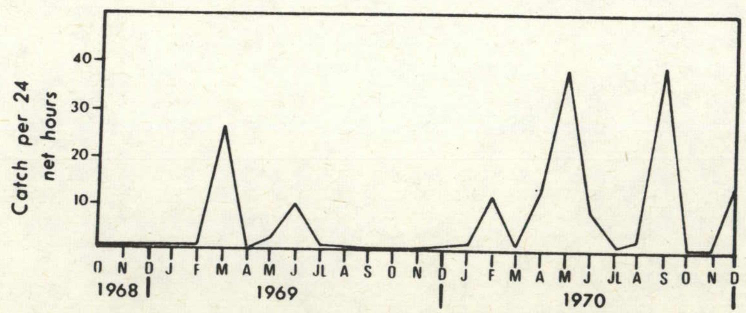


FIG. 3 SEASONAL ABUNDANCE OF ADULT *M. cephalus* IN St LUCIA SOUTH LAKE.