ISSN 0073-4381

ICHTHYOLOGICAL BULLETIN

of the

J.L.B. SMITH INSTITUTE OF ICHTHYOLOGY

GRAHAMSTOWN, SOUTH AFRICA

NUMBER 57 JUNE 1992

RECRUITMENT OF JUVENILE MARINE FISHES INTO PERMANENTLY OPEN AND SEASONALLY OPEN ESTUARINE SYSTEMS ON THE SOUTHERN COAST OF SOUTH AFRICA

by

A. K. Whitfield and H. M. Kok

ABSTRACT

Whitfield, A.K. & H.M. Kok. 1992. Recruitment of juvenile marine fishes into permanently open and seasonally open estuarine systems on the southern coast of South Africa. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* No. 57, 39 pages, 4 figures, 1 appendix (22 bar graphs).

The recruitment of juvenile marine fishes into the Knysna and Swartvlei estuaries was monitored over 30 months using seine, scoop and cast nets. The relative abundance, seasonality and growth of the dominant species are presented, and includes the Cape stumpnose *Rhabdosargus holubi,* white steenbras *Lithognathus lithognathus,* blacktail *Diplodus sargus,* strepie *Sarpa salpa,* Cape moony *Monodactylus falciformis,* southern mullet *Liza richardsonii,* groovy mullet *Liza dumerilii,* striped mullet *Liza tricuspidens,* flathead mullet *Mugil cephalus,* freshwater mullet *Myxus capensis* and leervis *Lichia amia.* Information on a further 12 species is also provided.

Recruitment of most fish species into the Swartvlei and Knysna estuaries reaches a peak during summer, which coincides with maximum food resource availability and corresponds to the time when systems along this section of the coast are often open to the sea. Artificial winter breaching of the Swartvlei mouth has occurred in the past, and has generally led to the premature closure of the system and loss of the 'head' of water needed for the summer opening. This type of mouth manipulation leads to reduced availability of estuarine nursery areas for marine fishes along the southern Cape coast.

Comparisons between the recruitment of juvenile fishes into the Knysna and Swartvlei estuaries indicate that higher densities of most species were recorded in the former system. This is attributed mainly to the fact that the Knysna mouth is deep, permanently open, and has a strong marine influence when compared to the shallow, narrow and seasonally closed Swartvlei mouth. However, in a regional context both Knysna and Swartvlei are large, unpolluted systems, which serve as important nursery areas for many species of fish. On this basis alone, these contrasting estuarine systems should be allocated the highest possible conservation status.

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ISBN 0-86810-235-0

RECRUITMENT OF JUVENILE MARINE FISHES INTO PERMANENTLY OPEN AND SEASONALLY OPEN ESTUARINE SYSTEMS ON THE SOUTHERN COAST OF SOUTH AFRICA

by

A.K. Whitfield[1] and H.M. Kok[2]

INTRODUCTION

Studies in southern Africa and elsewhere have shown that the overwhelming majority of fish species found in estuaries are of marine origin (Blaber, 1981; Yanez-Arancibia, 1985). Some of these species are able to complete their life cycles in estuaries and are termed residents, but most may be classified as marine migrants (Day *et al.*, 1981). Typically the migrant species spawn and complete their early stages of development in the sea, which is a less stressful environment for fish eggs and larvae when compared to conditions in estuaries (Wallace, 1975a; Whitfield, 1990).

Postflexion larvae and 0+ juveniles of many marine fishes migrate actively into estuaries where they remain for varying lengths of time before returning to the marine environment, prior to, or after attaining sexual maturity (Wallace 1975b; Potter *et al.*, 1990). This type of life cycle has led to estuaries being termed 'nursery areas' and is reflected in the very large numbers of small juvenile fish in the littoral waters of these systems (Beckley, 1983; Blaber, 1987). The reliance of juveniles of migrant marine species on estuarine nursery grounds varies considerably, and ranges from marine stragglers which are seldom found in estuaries, to those species that are dependent on estuaries during the juvenile phase of their life cycle (Wallace *et al.*, 1984a). Some species such as the southern mullet *Liza richardsonii*, white stumpnose *Rhabdosargus globiceps* and elf *Pomatomus saltatrix*, appear to use favourable estuarine conditions opportunistically, the juveniles also being very abundant in the sea. Other species, like the white steenbras *Lithognathus lithognathus*, Cape stumpnose *Rhabdosargus holubi* and Cape moony *Monodactylus falciformis*, are considered to be dependent on estuarine nursery grounds and might even become extinct if denied access to these areas (Bennett *et al.*, 1985).

Recruitment of juvenile marine fishes into southern African estuaries has been investigated by a number of ichthyologists (e.g. Wallace & van der Elst, 1975; Whitfield, 1980; Beckley, 1984a). Although certain authors (viz. Bennett *et al.*, 1985; Kok & Whitfield, 1986) have documented the changes within a fish community arising from mouth opening and closing, only one study in South Africa (Bennett, 1989) has compared the fish communities in nearby permanently open, seasonally open and normally closed estuaries. A primary aim of the present study was to compare the recruitment of 0+ juveniles into two relatively large estuarine systems; the permanently open Knysna estuary and the seasonally open Swartvlei estuary. Apart from documenting major immigration phases for selected marine species into these estuaries, this paper also estimates the growth of dominant 0+ juveniles in estuarine nursery areas.

STUDY AREAS

The Knysna and Swartvlei estuaries are situated 25 km apart on the southern Cape* coast (Fig. 1) and both are fed by rivers arising in the Outeniqua Mountains. The mean annual run-off of the Knysna catchment is between 70-133 x 10^6 m^3 (Grindley, 1985), whereas that of the Swartvlei catchment is approximately 66 x 10^6 m^3 (Whitfield *et al.*, 1983). Although the river gradients in both systems are steep, erosion on the forested slopes is minimal, and the river waters are clear though peat-stained. Small weirs and causeways have been built across the rivers of both systems but no major dams have as yet been constructed.

The permanently open Knysna estuary (Fig. 2a) is about 19 km long and gradually broadens to form a lagoon over 3 km wide and up to 6 m deep. The mouth of the estuary opens between two rocky headlands that prevent longshore drift of sand into the lagoon (Day, 1981). Depths of up to 16 m have been recorded in the mouth channel (Grindley, 1985). In contrast, the seasonally closed Swartvlei estuary (Fig. 2b) is about 7 km long, but is linked to an estuarine lake (Swartvlei) which is 8.8 km^2 in area with a maximum depth of 16 m. The estuary itself is very shallow (maximum depth = 4 m) with a narrow central channel bordered by intertidal sand flats of varying widths. The sediments of the entire estuary consist of recently deposited dune sands, with the exception of the mouth area where dune rock borders the eastern shore. The mouth of the estuary is frequently closed during winter (Fig. 3) due to southwesterly wave action which is predominantly responsible for sand transport along this coast (Whitfield *et al.*, 1983). Artificial opening of the mouth is normally carried out mechanically when the water level behind the sand bar reaches 1.8-2.0 m above mean sea level.

The spring tidal range along the south coast is approximately 1.8 m, and although there is some amplitude reduction in the broad Knysna lagoon, this range persists more than half-way up the estuary (Day, 1981). In contrast, only 0.5 km from the Swartvlei mouth, the tidal range is reduced by one third (Whitfield *et al.*, 1983).

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* In this paper, Cape is used as a synonym for the Cape Province of South Africa.

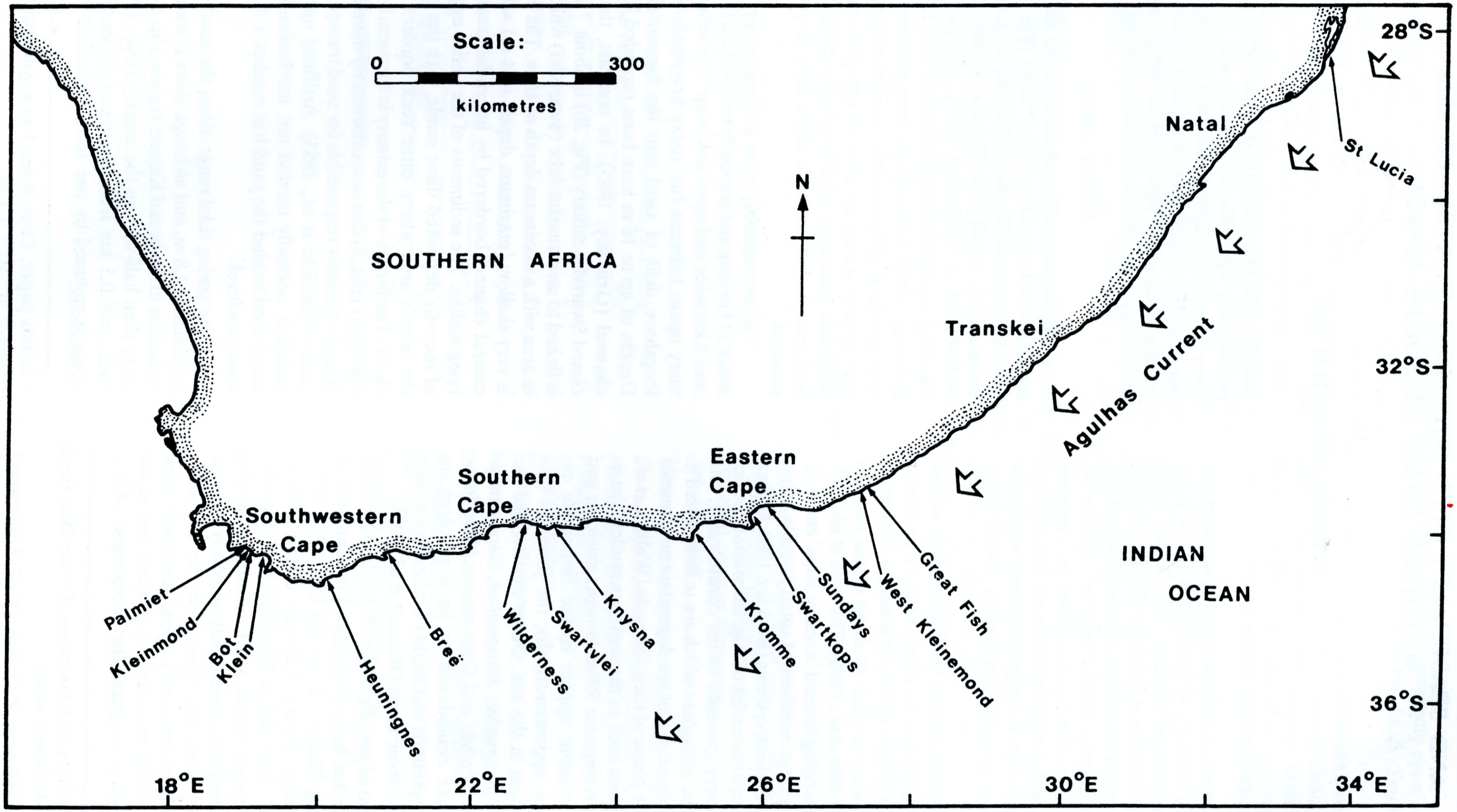

Figure 1. Map of southern Africa showing the localities of estuarine systems mentioned in the text.

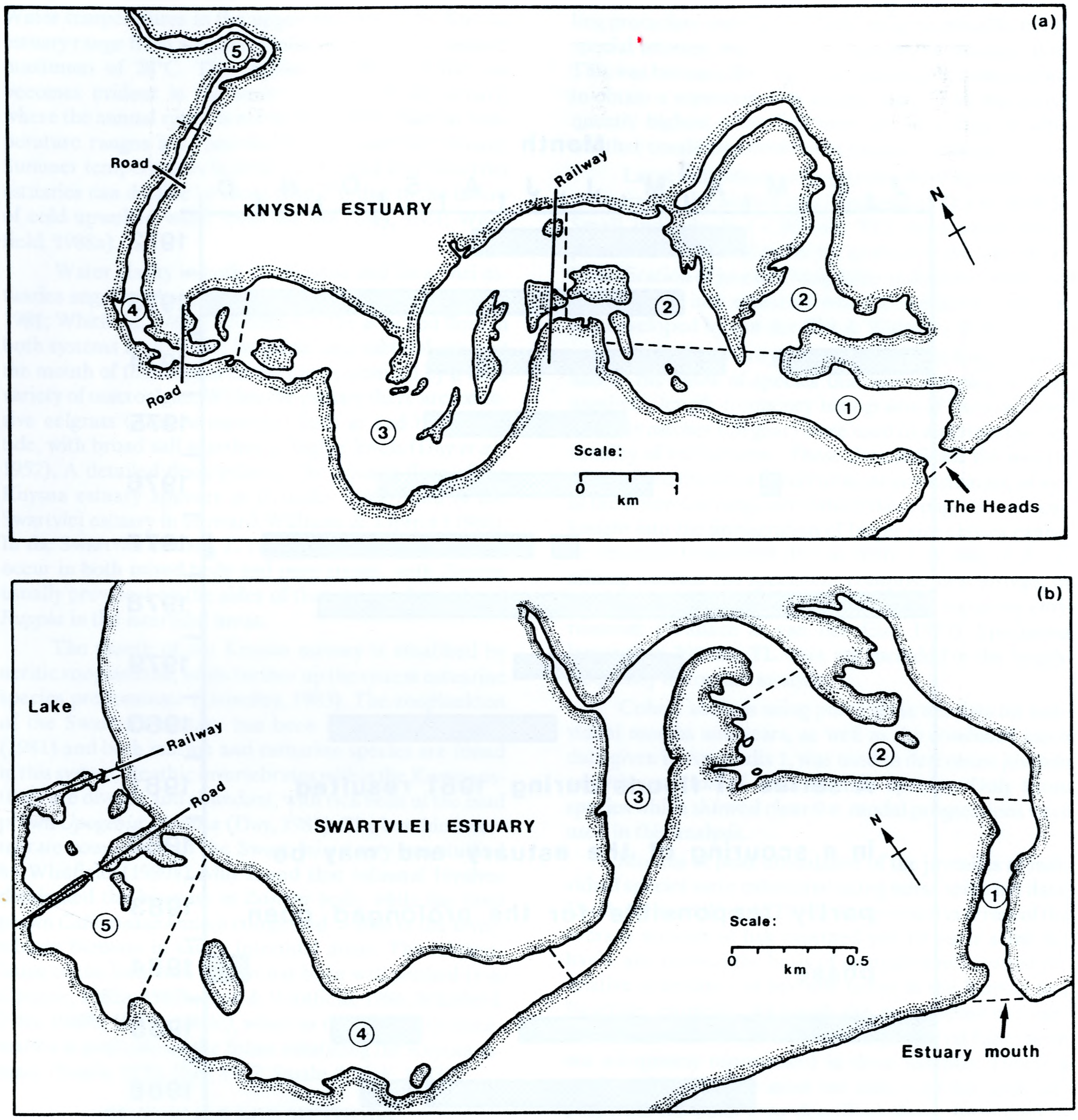

Figure 2. The Knysna (a) and Swartvlei (b) estuaries showing the five sampling regions in each system.

Tidal water currents up to 1.6 m s^{-1} have been recorded in both the Knysna and Swartvlei estuaries.

At the Charlesford rapids, which mark the head of the Knysna estuary, the water is well stratified with salinities of < 1 g kg^{-1} on the surface and 5 g kg^{-1} at the bottom. However, the normal river discharge is insignificant when compared with the tidal exchange at the mouth, so that the isohalines rapidly become steeper downstream of the headwaters. Salinities of 30-35 g kg^{-1} are recorded at the rail bridge and seaward of this point there is little indication of vertical gradients (Day, 1981). In the Swartvlei estuary, salinities in the middle and upper reaches normally range between 15 and 35 g kg^{-1} during the tidal phase, whereas those in the lower reaches fluctuate between 25 and 35 g kg^{-1} (Whitfield, 1988a). Salinities above 30 g kg^{-1} can occur throughout the Swartvlei estuary immediately prior to and after mouth closure. Salinity then declines during the closed phase as water from Swartvlei lake moves into the estuary, and the water level of the system rises. Minimum salinities (< 5 g kg^{-1}), which are of short duration (< 10 days), occur when the mouth is open and the rivers are flooding.

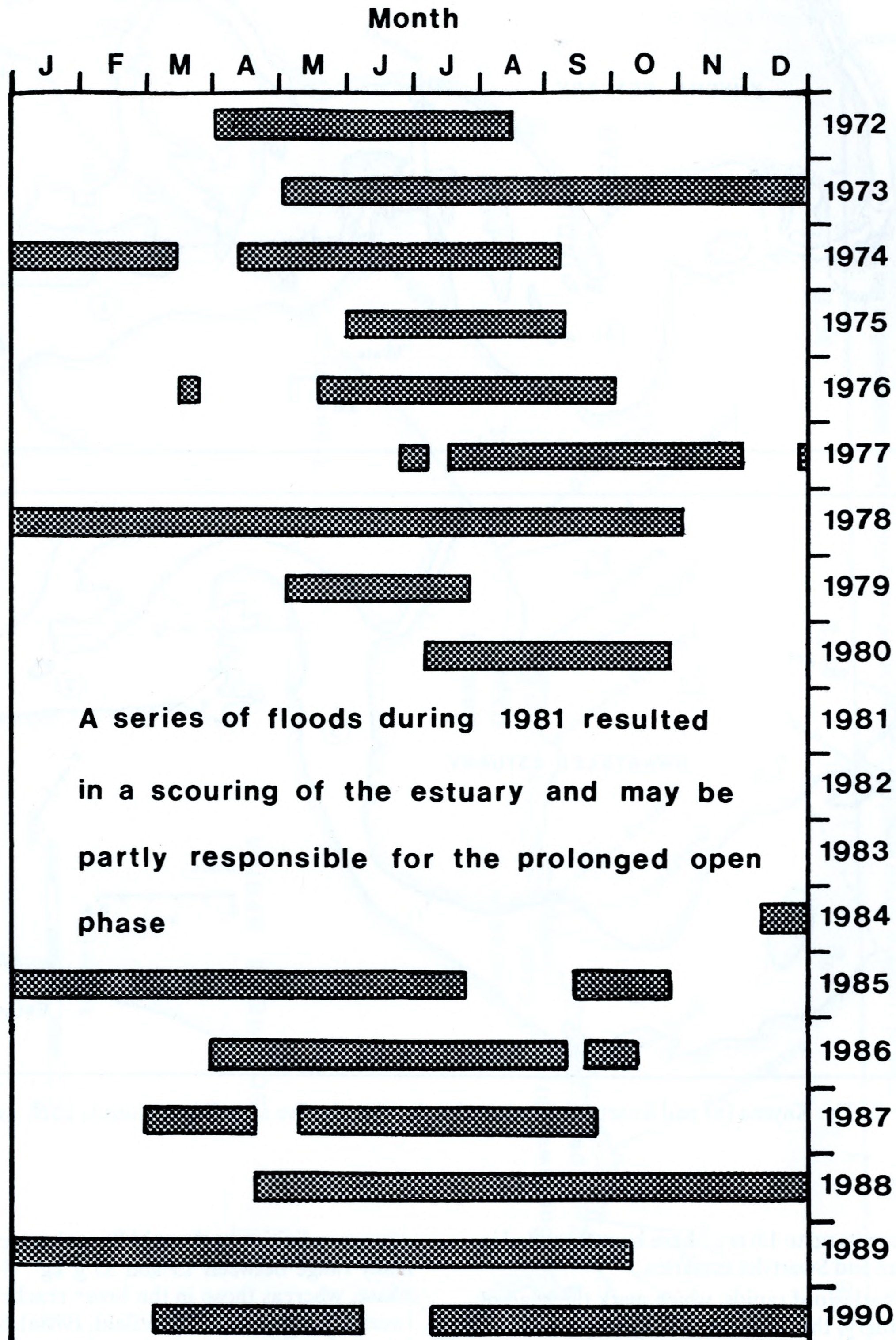

Figure 3. A 19-year record of periods when the Swartvlei estuary was closed (hatched bars).

Water temperatures in the upper reaches of the Knysna estuary range from a winter minimum of 13° to a summer maximum of 28°C. The stabilising effect of the sea becomes evident in the lower reaches of the estuary, where the annual range is normally 15-23°C. Similar temperature ranges are recorded in the Swartvlei estuary. Summer temperatures in both the Knysna and Swartvlei estuaries can decline by more than 7°C due to the inflow of cold upwelled water from the sea (Day, 1981; Whitfield, 1988a).

Water clarity in both the Knysna and Swartvlei estuaries suggests that phytoplankton biomass is low (Day 1981; Whitfield, 1988a). In contrast, the attached flora in both systems is rich. The intertidal and subtidal areas at the mouth of the Knysna estuary are colonised by a wide variety of macroalgae. Within the estuary there are extensive eelgrass (*Zostera capensis*) beds at and below low tide, with broad salt marshes at higher levels (Day *et al.*, 1952). A detailed description of the aquatic flora of the Knysna estuary appears in Grindley (1985) and of the Swartvlei estuary in Howard-Williams & Liptrot (1980). In the Swartvlei estuary, *Z. capensis* and *Ruppia cirrhosa* occur in both mixed beds and pure stands, with *Zostera* usually prevalent on the sides of the estuary channel and *Ruppia* in the intertidal areas.

The mouth of the Knysna estuary is inhabited by neritic zooplankton, while further up the system estuarine species predominate (Grindley, 1985). The zooplankton of the Swartvlei estuary has been studied by Coetzee (1981) and both marine and estuarine species are found in this system. Benthic invertebrates within the Knysna estuary are diverse and abundant, with rich beds of the mud prawn *Upogebia africana* (Day, 1981). The benthic invertebrate community of the Swartvlei estuary was studied by Whitfield (1989a) who found that infaunal bivalves dominated the biomass in *Zostera* beds, while the sand prawn *Callianassa kraussi* comprised >80% of the invertebrate biomass in sandy intertidal areas. The ichthyofauna of the Swartvlei system has been well studied (e.g. Coetzee, 1982a; 1982b; Kok & Whitfield, 1986; Whitfield, 1986; 1988b; 1989b; 1989c), whereas relatively little information is available on the fishes inhabiting the Knysna estuary (Smith, 1933; Day, 1967; Smale & Kok, 1983).

MATERIALS AND METHODS

Five types of gear, similar to that used by Wallace & van der Elst (1975) in Natal, were used to sample the fish community of the Knysna and Swartvlei estuaries. A fry seine net (3 m long, 1 m deep, with a 2 mm bar mesh) and 50 cm diameter fry scoop net (2 mm bar mesh) were used in shallow waters less than 0.5 m deep. A small seine net (5 m long, 2 m deep, with a 6 mm bar mesh) and cast net (3 m diameter, 12 mm bar mesh) were used in water up to 1.5 m deep and a purse seine net (30 m long x 2 m deep with a 6 mm bar mesh in the purse) in water up to 3 m deep. The various gear made it possible to sample a variety of habitats, including both vegetated and non-vegetated littoral areas.

Netting was conducted monthly, during daylight hours, between July 1978 and December 1980. The sampling procedure was standardised as far as possible, but no special attempt was made to standardise netting effort. This was because the objective of each collecting trip was to obtain a representative sample, and effort was consequently highest when fish were not abundant or when weather conditions made their capture difficult.

Large individuals in the catches were identified and measured to the nearest mm total length (TL) in the field. Small individuals (<50 mm TL) were immediately preserved in 10% formalin for analysis in the laboratory. Identification of juvenile Mugilidae at the stage when they first migrate into estuaries was accomplished using the key developed by van der Elst & Wallace (1976).

Catch data were grouped into 10 mm length classes and in the cases of species that were sampled in large numbers, length-frequency histograms of the combined monthly catches (all gear) were used to ascertain the seasonality of recruitment. These data indicate the months of onset and duration of recruitment into estuaries, as well as the lower size range over which these migrations occur. 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 (Wallace & van der Elst, 1975). Specimens larger than 290 mm TL were not included in the length-frequency histogram analysis.

Cohort analysis using purse seine net data for individual months and years, as well as the combined catch data given in Appendix 1, was used to determine juvenile growth patterns of selected fish species. Only those species which showed clear 0+ modal progressions were used in this analysis.

Months of peak abundance of the juveniles of individual species were calculated using purse seine net data. Catch per unit effort (CPUE) is expressed in terms of the average number of fish captured per 10 purse seine net hauls, and formed the basis of comparisons between the relative abundance of juvenile fishes in the Knysna and Swartvlei estuaries. Although the purse seine net captured a wide size range of juveniles, postlarval fishes were not adequately represented in these samples. Hence a combination of purse seine net data, together with catches from the other gear described above, were used to ascertain periods of peak recruitment into the individual estuaries.

Information on the abundance and seasonality of estuarine associated species in the Swartvlei Bay surf zone was obtained from data used in a study by Whitfield (1989d). Scientific nomenclature follows that used in Smith & Heemstra (1991).

RESULTS AND DISCUSSION

DOMINANT SPECIES

Rhabdosargus holubi (Family: Sparidae)

In Natal this species spawns in the marine environment between May and August (Wallace, 1975a) and information from the eastern Cape supports a winter/spring spawning peak (Blaber, 1974a). Data from the Swartvlei

Bay marine environment suggests a peak in *R. holubi* postflexion larval abundance during summer and a decline in densities during winter. *R. holubi* <40 mm TL were recorded throughout the year in both the Knysna and Swartvlei estuaries (Appendix 1: Bar Graphs 1 & 2). The major periods of recruitment into southern Cape estuaries were from August to April and were discernible from the monthly length-frequency histograms.

In the temporarily open West Kleinemond estuary, Blaber (1974a) recorded a spring/summer influx of 0+ *R. holubi*. Melville-Smith & Baird (1980) and Beckley (1983), working in the permanently open Swartkops estuary, found specimens <20 mm TL throughout the year, with a marked influx of 0+ juveniles in early summer. Postlarval *R. holubi* were most abundant in the Sundays River estuary during November (Harrison & Whitfield, 1990), and juveniles attained high densities in Swartkops estuary *Zostera* beds between September and March (Beckley, 1983). On the southwestern Cape coast, recruitment of 15-40 mm TL *R. holubi* into the Palmiet and Kleinmond estuaries occurred between October and April (Bennett, 1989).

In Natal, *R. holubi* of 10-20 mm TL start migrating into estuaries during July, with large numbers of 20-40 mm specimens following in August. According to Wallace & van der Elst (1975) the main recruitment period for 10-40 mm length classes extends from July to November, with some immigration of 30-40 mm juveniles continuing as late as January. Therefore, it would appear that peak *R. holubi* immigration into Natal estuaries begins and ends earlier than that in Cape estuaries.

A monthly growth increment of 8 mm was estimated for *R. holubi* 0+ juveniles in Zululand estuaries between August and January, and led Wallace & van der Elst (*op. cit.*) to conclude that *R. holubi* in these systems attain 100 mm in their first year. Annual modal progressions of 0+ juveniles from the Knysna estuary (Appendix 1: Bar Graph 1) also indicate a growth of approximately 100 mm in their first year, whereas those from the Swartvlei estuary (Appendix 1: Bar Graph 2) do not provide a clear modal series suitable for the estimation of juvenile growth rate. According to Beckley (1983) growth of *R. holubi* in the Swartkops estuary is rapid to about 80 mm when numbers become too low to follow the cohorts in the study creek. Winter (1979) estimated that *R. holubi* in the same estuary attained 100 mm in their first year, which is also similar to the findings of Beckley (1984a) in the Sundays River estuary. Using tagged fish recoveries, Blaber (1974a) recorded a summer (September-March) growth rate of 10.3 mm per month and a winter (April-August) growth rate of 3.5 mm per month.

R. holubi was abundant in the middle and upper reaches of both the Knysna and Swartvlei estuaries. The species was also a dominant component in the littoral zone of Swartvlei lake (Whitfield, 1984) and is closely associated with eelgrass beds in the Knysna and Swartvlei estuaries (Whitfield *et al.*, 1989). Hanekom & Baird (1984), working in the Kromme estuary, recorded significantly higher numbers of juvenile *R. holubi* in *Zostera* than in non-*Zostera* areas.

Lithognathus lithognathus (Family: Sparidae)

This species spawns mainly between June and August (Mehl, 1973). *L. lithognathus* <40 mm TL were recorded entering the Knysna estuary between September and January, with a November peak in both the Knysna and Swartvlei estuaries (Appendix 1: Bar Graphs 3 & 4; Table 1). This is similar to the October peak recorded by Beckley (1984a) in the Sundays River estuary. The largest numbers of *L. lithognathus* in the Knysna and Swartvlei estuaries occurred in the middle and upper reaches.

Annual modal progressions of 0+ juveniles from the Knysna estuary (Appendix 1: Bar Graph 3) indicated a growth of approximately 140 mm in their first year and is similar to that recorded by Beckley (1984a) in the Sundays River estuary. Sample sizes of *L. lithognathus* from the Swartvlei estuary (Appendix 1: Bar Graph 4) were too small to provide meaningful annual growth estimates, but indications were that 10-20 mm October recruits attained 140-150 mm by July (i.e. 130 mm in 10 months). The above estimates are considerably higher than the 60 mm 0+ annual growth recorded by Blaber (1974a) in the closed West Kleinemond estuary.

Recruitment into the temporarily open Kleinmond estuary on the southwestern Cape coast took place in November and December 1980, at which time fish length ranged from 18-50 mm TL (Bennett, 1989). By April 1981, when sampling ceased, these recruits had grown to a mean length of 125 mm. Based on this and other data, Bennett (*op. cit.*) estimated that *L. lithognathus* attain 160 TL mm in their first year. Mehl (1973), working in the nearby Heuningnes estuary, estimated a first year growth of 100 mm FL using otolith and scale annuli.

Diplodus sargus capensis (Family: Sparidae)

Although *D. sargus* is primarily a marine inshore species favouring tidal pools and inshore reefs as nursery areas (Smale & Buxton, 1989), 0+ juveniles are frequently abundant in southern African estuaries (Beckley, 1983). This species has a protracted breeding season with peak spawning activity from July-September in Natal (Joubert, 1981) and October-December in the Cape (Coetzee, 1986).

Data from the Swartvlei Bay surf zone indicates a peak in postflexion larval abundance from October to December. Lasiak (1983a) recorded *D. sargus* <50 mm TL throughout the year in the Algoa Bay surf zone, with an abundance peak in February. Summer recruitment of *D. sargus* juveniles into eastern Cape intertidal pools has been documented by Beckley (1985a), and according to Smale & Buxton (1989) *D. sargus* <40 mm TL entered subtidal gullies in the same region mainly during February and March.

Estuarine recruitment follows a similar pattern to that described for the marine inshore environment. *D. sargus* <40 mm TL were recorded entering the Knysna estuary mainly during the spring and summer months, with a peak in recruitment of these size classes between October and December (Appendix 1: Bar Graph 5). In the Swartvlei estuary, recruitment commenced in October and lasted until April (Appendix 1: Bar Graph 6), but CPUEs were lower compared to the Knysna estuary (Table 1). Beckley (1983) documented an influx of 0+ juveniles into the Swartkops estuary in spring and early summer, and Bennett (1989) recorded recruitment of *D. sargus* into two southwestern Cape estuaries during March and May. However, the length at recruitment into the Palmiet and Kleinmond estuaries was 40-60 mm compared to < 40 mm in southern and eastern Cape estuaries.

Smale & Buxton (1989) followed monthly cohort progressions in subtidal gullies and estimated that *D. sargus* attained 100-120 mm TL in one year. Monthly catches from the Knysna and Swartvlei estuaries did not provide a clear modal series suitable for the estimation of juvenile growth rates. Similarly, Beckley (1983) was unable to follow the growth of individual cohorts in the Swartkops estuary.

Densities of *D. sargus* were greatest in the lower and middle reaches of the Knysna and Swartvlei estuaries, with few individuals penetrating the upper reaches of these systems.

Sarpa salpa (Family: Sparidae)

Spawning by this species occurs between April and September, with months of peak activity being June to August (Joubert, 1981). Evidence presented by Joubert (*op. cit.*) suggests that *S. salpa* spawns in deep water off the Natal coast and the larvae drift southward with the Agulhas Current. Juveniles < 40 mm TL were recorded entering the Algoa Bay surf zone in August and September (Lasiak, 1983a), and postlarvae 15-30 mm TL have been recorded in the Swartvlei Bay surf zone between May and September (Whitfield, 1989d). Recruitment of *S. salpa* < 30 mm TL into eastern Cape tide pools takes place between June and September (Christensen, 1978) with juveniles > 50 mm TL occurring in subtidal gullies from November-July (Smale & Buxton, 1989). Entry of 13-60 mm TL *S. salpa* into the Swartkops estuary was recorded in October (Beckley, 1985b), and 13-80 mm TL specimens occupied eelgrass beds in this estuary between July and February (Beckley, 1983).

Peak recruitment of 0+ *S. salpa* into the Knysna estuary occurred between September and December, and in the Swartvlei estuary between October and December (Appendix 1: Bar Graphs 7 & 8; Table 1). Cohort analyses from the Knysna estuary (Appendix 1: Bar Graph 7) indicated a growth of approximately 140 mm in the first year, which was similar to the 12 mm per month estimated by Lasiak (1983a) for the 40-100 mm length classes in Algoa Bay. Modal progressions from eastern Cape subtidal gullies suggest that *S. salpa* may attain 120 mm after one year (Smale & Buxton, 1989).

S. salpa is a herbivorous species which is closely associated with the eelgrass beds in the lower and middle reaches of the Knysna and Swartvlei estuaries (Whitfield *et al.*, 1989). It appears to be absent from the upper reaches of both systems, even though submerged macrophyte beds are present in these areas.

Liza richardsonii (Family: Mugilidae)

According to Lasiak (1983b) *L. richardsonii* spawns in eastern Cape waters between September and March, often close inshore (van der Host & Erasmus, 1981). Unlike most other mugilids, which rely mainly on estuarine nursery areas (Wallace *et al.*, 1984a), the juveniles of this species are abundant both in estuaries (Beckley, 1984a) and in the marine habitat (Romer & McLachlan, 1986). In the Knysna and Swartvlei estuaries they are most abundant in the lower and middle reaches. They do, however, penetrate the upper reaches of estuaries, and Whitfield (1986) recorded moderate numbers in the littoral zone of Swartvlei lake.

Peak abundance of mugilid postflexion larvae in the Swartvlei Bay surf zone was between October and March, which coincided with the recruitment of *L. richardsonii* < 20 mm TL into the Swartvlei estuary. It would appear, however, that juvenile recruitment into both the Knysna and Swartvlei (when the mouth was open) estuaries occurred throughout the year, with peak immigration (CPUE) between November and May (Appendix 1: Bar Graphs 9 & 10; Table 1). Large numbers of *L. richardsonii* 10-40 mm SL were recorded migrating up the Wilderness estuarine system during February (Hall *et al.*, 1987).

Cohort analysis of *L. richardsonii* in the Knysna and Swartvlei estuaries was not possible due to the extended recruitment period and lack of distinctive age classes. Although the larval development of this species has been described (Cambray & Bok, 1989), no published information on juvenile growth rates is available.

Liza tricuspidens (Family: Mugilidae)

This species spawns mainly between August and November in Natal waters, but very few juveniles have been recorded in adjacent estuaries (Wallace, 1975a; Wallace & van der Elst, 1975). In the eastern Cape, however, *L. tricuspidens* < 100 mm TL have been recorded in moderate numbers from the Sundays and Swartkops estuaries (Beckley, 1983; 1984a), as well as from tidal pools in the area (Beckley, 1985a).

Juveniles first enter estuaries at a length of 20-30 mm TL (Wallace & van der Elst, 1975; Beckley, 1983; 1984a; Appendix 1: Bar Graphs 11 & 12) and according to Blaber (1987) recruitment occurs between November and January. Evidence from our study (Appendix 1: Bar Graphs 11 & 12; Table 1) suggests an October-May influx of 0+ juveniles into the Knysna and Swartvlei estuaries, with peak recruitment between October and December. Cohort analysis from the Knysna system (Appendix 1: Bar Graph 11) indicates that *L. tricuspidens* may attain 140 mm TL in their first year.

In the Knysna and Swartvlei systems, this species is most abundant in the lower half of the estuaries, with relatively few individuals penetrating the upper reaches. A similar situation pertains to the nearby Wilderness system, where *L. tricuspidens* was restricted to the Wilderness lagoon and did not utilize the adjoining estuarine lakes (Hall *et al.*, 1987).

Table 1. Average monthly catch per unit effort (number of fish per 10 purse seine net hauls)

Family	Species	Jul	Aug	Sep	Oct	Nov	Dec
Sparidae:	*Diplodus sargus*	0.6	1.1	11.0	4.3	23.8	21.6
		1.5	0.1	0.2	1.1	4.1	19.6
	Diplodus cervinus	0.0	0.1	0.2	0.2	1.3	1.6
		0.0	0.0	0.0	0.0	0.9	0.6
	Lithognathus lithognathus	13.4	4.9	8.1	10.1	31.0	10.5
		26.5	8.3	9.6	6.0	30.4	17.7
	Lithognathus mormyrus	0.0	0.4	0.1	1.5	1.7	1.9
		0.0	0.0	0.0	0.0	0.0	0.0
	Rhabdosargus holubi	28.5	65.1	41.0	38.7	42.5	30.8
		29.4	75.4	47.9	60.2	136.9	116.4
	Rhabdosargus globiceps	0.0	0.0	0.0	0.0	0.0	0.0
		0.0	0.3	1.1	0.5	0.8	1.9
	Sarpa salpa	1.4	4.7	12.5	20.8	35.5	24.8
		7.4	0.1	0.8	33.8	23.3	22.5
	Spondyliosoma emarginatum	0.0	0.0	0.0	0.0	6.2	15.5
		0.0	0.0	0.0	0.0	0.7	4.2
Mugilidae:	*Liza dumerilii*	1.5	5.2	5.6	8.1	4.0	7.1
		0.0	0.0	0.9	0.6	6.5	1.8
	Liza richardsonii	9.8	6.5	6.1	4.4	9.8	8.0
		1.3	3.9	7.9	14.6	17.7	5.5
	Liza tricuspidens	0.2	0.2	1.3	0.0	0.3	1.9
		0.0	0.0	0.0	0.0	2.1	5.2
	Mugil cephalus	0.2	1.0	0.1	2.2	0.2	0.3
		0.7	0.0	0.1	0.0	0.1	0.3
	Myxus capensis	0.0	0.0	0.6	0.1	0.4	0.3
		0.0	0.0	0.0	0.0	0.7	0.1
	Valamugil buchanani	0.0	0.0	0.0	0.1	0.0	0.0
		0.0	0.0	0.0	0.0	0.0	0.0
Soleidae:	*Heteromycteris capensis*	0.0	2.6	0.4	0.1	0.1	0.3
		0.4	0.0	0.0	0.4	0.0	0.0
	Solea bleekeri	0.2	3.0	0.3	0.2	0.3	0.2
		0.2	0.4	0.1	1.2	0.1	0.2
Haemulidae:	*Pomadasys commersonnii*	0.0	0.0	0.2	0.5	0.0	0.0
		0.0	0.0	0.1	0.0	0.0	0.0
	Pomadasys olivaceum	0.0	0.0	0.0	0.0	0.3	4.9
		0.0	0.0	0.0	0.0	0.0	0.0
Monodactylidae:	*Monodactylus falciformis*	30.2	1.0	0.6	0.5	4.2	3.8
		10.7	5.7	4.7	0.4	3.2	6.4
Hemiramphidae:	*Hemiramphus far*	0.0	0.0	0.0	0.0	0.4	0.6
		0.0	0.0	0.0	0.0	0.0	0.0
Carangidae:	*Lichia amia*	0.0	0.0	0.2	0.0	0.2	0.2
		0.0	0.6	0.0	0.3	0.0	0.2
Pomatomidae:	*Pomatomus saltatrix*	0.0	0.0	0.0	0.8	0.3	1.0
		0.0	0.0	0.0	0.0	0.0	0.0

in the Knysna and Swartvlei estuaries.

Jan	Feb	Mar	Apr	May	Jun	Mean	Locality
21.2	25.0	28.5	16.6	3.3	0.5	13.1	Knysna
14.9	14.0	10.3	3.7	2.8	8.7	6.8	Swartvlei
1.7	0.9	0.9	0.1	0.1	0.0	0.6	Knysna
0.1	0.1	0.1	0.5	0.0	0.3	0.2	Swartvlei
22.8	39.6	17.7	17.1	4.2	2.5	15.2	Knysna
11.1	11.0	8.7	47.4	19.1	15.3	17.6	Swartvlei
4.9	2.2	10.3	0.2	0.6	0.0	2.0	Knysna
0.0	0.0	0.0	0.0	0.1	0.0	0.0	Swartvlei
36.5	49.7	55.7	110.0	30.1	3.4	44.3	Knysna
75.5	101.5	109.6	137.8	122.9	223.1	103.1	Swartvlei
0.0	0.1	0.7	0.1	0.1	0.0	0.1	Knysna
4.4	4.2	1.1	0.3	0.3	0.1	1.3	Swartvlei
23.3	11.0	12.3	12.4	6.8	0.0	13.8	Knysna
0.4	1.7	0.0	0.3	0.1	12.6	8.6	Swartvlei
11.7	7.1	24.9	4.1	2.0	0.0	6.0	Knysna
0.5	1.6	0.0	0.1	0.0	0.0	0.6	Swartvlei
7.7	6.4	29.7	15.0	11.1	70.2	14.3	Knysna
24.7	18.2	9.9	2.6	4.5	0.4	5.8	Swartvlei
5.9	4.1	3.1	7.9	14.0	6.6	7.2	Knysna
18.0	30.5	36.8	21.4	24.6	11.0	16.1	Swartvlei
1.2	0.1	1.4	2.2	1.8	0.7	0.9	Knysna
9.4	4.0	1.4	0.2	0.0	0.0	1.9	Swartvlei
0.5	0.8	0.2	0.0	0.3	0.2	0.5	Knysna
0.1	0.7	0.5	0.2	0.0	0.0	0.2	Swartvlei
0.5	0.6	0.9	0.1	2.5	0.0	0.5	Knysna
0.1	0.5	0.3	0.1	0.3	0.0	0.2	Swartvlei
0.0	0.0	0.0	0.0	0.0	1.3	0.1	Knysna
0.0	0.0	0.0	0.0	0.0	0.0	0.0	Swartvlei
0.0	0.0	0.4	0.4	0.6	0.1	0.4	Knysna
0.5	0.0	0.5	0.0	0.0	0.4	0.2	Swartvlei
0.2	0.1	0.2	0.3	0.3	0.2	0.5	Knysna
0.1	0.1	0.4	0.0	0.5	0.4	0.3	Swartvlei
0.0	0.0	0.0	0.2	0.1	0.2	0.1	Knysna
0.0	0.0	0.0	0.0	0.0	0.0	0.0	Swartvlei
5.1	3.4	1.4	0.0	0.0	0.0	1.3	Knysna
0.0	0.0	0.0	0.0	0.0	0.0	0.0	Swartvlei
6.8	31.1	85.6	133.1	49.3	25.7	31.0	Knysna
2.4	21.2	21.4	21.7	3.3	66.9	14.0	Swartvlei
0.6	1.2	0.3	0.0	0.0	0.0	0.3	Knysna
0.0	0.0	0.6	0.0	0.0	0.0	0.1	Swartvlei
0.1	0.2	0.1	0.0	0.2	0.0	0.1	Knysna
0.0	1.1	0.0	0.0	0.0	0.1	0.2	Swartvlei
0.0	4.1	1.1	0.0	0.0	0.0	0.6	Knysna
0.0	0.0	0.0	0.0	0.0	0.0	0.0	Swartvlei

Liza dumerilii (Family: Mugilidae)

In Natal *L. dumerilii* breeds between June and November (Wallace, 1975a) but in the eastern Cape spawning occurs primarily between December and February (van der Horst & Erasmus, 1978; 1981). According to Wallace & van der Elst (1975) recruitment of specimens < 50 mm TL occurs mainly from August-February in Natal estuaries and April-May in eastern Cape estuaries (Beckley, 1984a). On the southern Cape coast, recruitment of *L. dumerilii* < 30 mm TL occurs throughout the year with a peak between November and June (Appendix 1: Bar Graphs 13 & 14).

Cohort analysis of *L. dumerilii* in the Knysna and Swartvlei estuaries was not possible due to the extended recruitment period and lack of distinctive age classes (Appendix 1: Bar Graphs 13 & 14). This species was most abundant in the lower and middle reaches of both the above estuaries, with moderate numbers also recorded in the upper reaches. *L. dumerilii* was an important component of the Swartvlei and Wilderness lakes fish faunas (Whitfield, 1986; Hall *et al.*, 1987).

Mugil cephalus (Family: Mugilidae)

This species spawns in the sea between May and September (Wallace, 1975a) with recruitment of < 30 mm TL juveniles into Natal estuaries occurring between June and October (Wallace & van der Elst, 1975). In eastern Cape estuaries, the main recruitment period of *M. cephalus* < 40 mm TL is June-October (Bok, 1979), with a peak during August/September (Beckley, 1984a). Recruitment of < 40 mm TL specimens into the Knysna estuary occurred from August to December, with a peak during September-November (Appendix 1: Bar Graph 15). Although recruitment of *M. cephalus* < 30 mm was recorded in the Swartvlei estuary during November (Appendix 1: Bar Graph 16), insufficient specimens were collected to determine immigration periodicity.

Cohort analysis indicates that < 40 mm specimens recruited into the Knysna estuary during August may attain 160 mm by the end of March (Appendix 1: Bar Graph 15). Extrapolation of the above growth data suggests a length of approximately 180 mm at the end of the first year. This is slightly less than the estimated growth rate of 0 + *M. cephalus* in Western Australian estuaries (Chubb *et al.*, 1981; Lenanton *et al.*, 1984) and in freshwater dams in the eastern Cape (Bok, 1984).

Flathead mullet were recorded throughout the Knysna and Swartvlei systems. In the eastern Cape this species regularly migrates up rivers (Bok, 1979) but there is no evidence to suggest a similar migration occurs into southern Cape freshwater areas. Only the freshwater mullet *Myxus capensis* has been recorded migrating up rivers in this region.

Myxus capensis (Family: Mugilidae)

The breeding season of this catadromous species extends from March-November, with the main recruitment period of < 20 mm FL juveniles taking place in the late winter and early summer months in the Kowie estuary (Bok, 1979). Data collected from the heads of other eastern Cape estuaries indicate a September-November peak in recruitment, although *M. capensis* fry < 30 mm FL were present in the upper reaches of the estuaries during most months of the year (Bok, 1984). In Natal estuaries, recruitment of 20-50 mm TL juveniles is reported to occur from August-December (Wallace & van der Elst, 1975).

Recruitment of < 30 mm TL *M. capensis* into the Knysna estuary was recorded throughout the year, with the main immigration period extending from July-November, and an October/November peak for these size classes (Appendix 1: Bar Graph 17). Recruitment into the Swartvlei estuary appeared poor compared to Knysna (Appendix 1: Bar Graphs 17 & 18; Table 1). This may be due to the timing and duration of the estuary mouth open phase, as well as postlarvae moving rapidly up into Swartvlei lake and adjacent rivers where sampling was not undertaken. Juveniles and adults of this species have been recorded from the lake during previous studies (Whitfield, 1986). The virtual disappearance of *M. capensis* > 60 mm TL from Knysna estuary catches (Appendix 1: Bar Graph 17) is probably due to their movement into the catchment rivers.

Cohort analysis in the Knysna estuary between November and January indicates an early juvenile growth rate of approximately 10 mm per month. According to Bok (1984) *M. capensis* attain 113 mm FL in one year and 211 mm FL after two years growth. Specimens 200-300 + mm TL captured in the Knysna estuary during March-May (Appendix 1: Bar Graph 17) were probably 2 + fish *en route* to the marine environment. Bok (1979) recorded a ripe-running *M. capensis* male (276 mm FL) in the surf zone adjacent to the Great Fish River estuary in April.

Monodactylus falciformis (Family: Monodactylidae)

The breeding season of *M. falciformis* extends from October to February, with evidence suggesting that this species is a serial spawner in Algoa Bay (Lasiak, 1984). Sampling in the Swartvlei Bay surf zone revealed an onshore movement of postflexion larvae < 7 mm TL between November and March.

Recruitment into the Knysna and Swartvlei estuaries occurs mainly during the summer months, with a peak between February and May at Knysna and February to April in the Swartvlei system (Appendix 1: Bar Graphs 19 & 20; Table 1). A similar summer recruitment pattern of *M. falciformis* entering the Swartkops estuary has been recorded by Melville-Smith & Baird (1980) and Beckley (1983). Plankton sampling indicates that entry into the Swartvlei estuary occurs at a length of < 10 mm TL (Whitfield, 1989b), whereas seine net catches suggest a length > 10 mm TL at first recruitment in both the Knysna and Swartvlei estuaries (Appendix 1: Bar Graphs 19 & 20).

According to Beckley (1984a), *M. falciformis* juveniles favour the vegetated upper reaches of estuaries, and specimens < 20 mm TL were particularly abundant in the *Potamogeton* beds of the upper Sundays River estuary between January and March. A similar abundance of juvenile *M. falciformis* has been recorded in *Potamogeton* beds in the upper reaches of the Swartvlei system

(Whitfield, 1984). In the Knysna estuary, this species is most abundant in the vicinity of *Ruppia* beds in the upper reaches and *Zostera* beds in the middle reaches. Hanekom & Baird (1984), working in the Kromme estuary, recorded significantly higher numbers of juvenile *M. falciformis* in *Zostera* than in non-*Zostera* areas.

Lichia amia (Family: Carangidae)

Spawning occurs off the Natal coast in spring and the Agulhas Current probably distributes the larvae southwards to the Cape (van der Elst, 1981). Very few juvenile *L. amia* have been recorded in Natal estuaries (Wallace, 1975b) and it would appear that this region is not an important nursery area for this species. First year juveniles occur in low numbers in eastern Cape estuaries, with initial summer recruitment taking place at a length of between 40 mm and 50 mm TL (Beckley, 1983; 1984a; Hanekom & Baird, 1984). Along the southwestern Cape coast, *L. amia* enters estuaries during December-March at a length of 50-120 mm TL (Bennett, 1989). On the southern Cape coast, Ratte (1982) captured leervis 50-80 mm FL in the Breë River estuary.

The recruitment period of 0+ juveniles is clearly defined in both the Knysna (November-January) and Swartvlei (December-January) estuaries. *L. amia* first enter these estuaries between 30 mm and 40 mm TL (Appendix 1: Bar Graphs 21 & 22), congregating in the shallows and preying on mysids, shrimps and small fishes (Smale & Kok, 1983). They are voracious predators and specimens < 80 mm FL frequently consume prey up to 70% of their body length (Smale & Kok, *op. cit.*). Growth is rapid and Blaber (1974a) recorded an 110 mm length increase in six months (January-July).

Juvenile *L. amia* were most frequently captured in the middle reaches of the Knysna estuary and lower reaches of the Swartvlei estuary. Subadult leervis are the dominant piscivorous fish species in Swartvlei lake (Whitfield, 1986) and estuary (Coetzee, 1982b).

OTHER SPECIES

Spondyliosoma emarginatum (Family: Sparidae)

This species is abundant in the nearshore marine environment (Buxton & Smale, 1984) but is restricted to the lower and middle reaches of Cape estuaries where it is associated with eelgrass beds (Whitfield *et al.*, 1989). The breeding season is from September through to January and males prepare nests in the coarse grit substratum around marine reefs (Penrith, 1972). Demersal eggs are laid in the nest and are protected by the parents until they hatch (Beckley, 1989).

Large numbers of the larvae (3-5 mm SL) were passively exchanged between the sea and the Swartvlei estuary during October and November 1986 (Whitfield, 1989b). However, juvenile recruitment into this estuary appears limited, with specimens < 50 mm TL being most abundant during November-February. In the Knysna estuary, large numbers of juveniles (10-50 mm TL) were recorded in the lower reaches between November and February. Beckley (1985b) recorded the immigration of 9-14 mm TL *S. emarginatum* into the Swartkops estuary during October.

Lithognathus mormyrus (Family: Sparidae)

This species is also primarily marine and makes limited use of estuaries (van der Elst, 1981). *L. mormyrus* is restricted to the lower and middle reaches of the Knysna estuary, and lower reaches of the Swartvlei system.

Juveniles < 40 mm TL were recorded in the Knysna estuary between September and April, and in the Swartvlei estuary between March and May. Lasiak (1983a) documented the presence of *L. mormyrus* juveniles < 50 mm TL in the Algoa Bay nearshore region throughout the year.

Rhabdosargus globiceps (Family: Sparidae)

In the southwestern Cape this species breeds in inshore waters between August and February, with a November/December spawning peak (Talbot, 1955). Recruitment of *R. globiceps* < 40 mm SL into the Klein River estuary occurred during January and February (Talbot, *op. cit.*), and January-April in the Palmiet and Kleinmond estuaries (Bennett, 1989). *R. globiceps* < 20 mm TL were recorded in the Swartvlei Bay surf zone during September and October (Whitfield, 1989d). Recruitment of < 40 mm TL specimens into the Knysna and Swartvlei estuaries occurred between September and December, with a November/December peak. Very few *R. globiceps* were captured in the upper reaches of these systems, and none were netted during a long-term study in Swartvlei lake (Whitfield, 1986).

Diplodus cervinus hottentotus (Family: Sparidae)

This inshore marine species (Beckley & Buxton, 1989) is regarded by Potter *et al.* (1990) as a marine straggler in Cape estuaries. Spawning on the southwestern Cape coast has been recorded from October-January (van der Elst, 1981) but recruitment of < 30 mm TL *D. cervinus* into the Knysna estuary occurred as early as September and extended into December. A similar pattern of recruitment was recorded in the Swartvlei estuary. Very few individuals penetrated the upper reaches of either the Knysna or Swartvlei estuaries. *D. cervinus* juveniles (< 75 mm TL) are abundant in shallow subtidal areas of the Tsitsikamma National Park (Buxton & Smale, 1984).

Solea bleekeri (Family: Soleidae)

This species breeds both in estuaries and the sea (Cyrus, 1991). Adults are common in the southern Cape inshore marine environment (Wallace *et al.*, 1984b) but relatively scarce in adjacent estuaries (Kok & Whitfield, 1986). Spawning occurs mainly between June and August in Natal waters (Wallace, 1975a), although recent evidence suggests that the breeding season in Lake St Lucia extends into the summer (Cyrus, 1991). Beckley (1986) recorded high densities of larval *S. bleekeri* (2-5 mm TL) in Algoa Bay during January and February, which coincided with the summer recruitment of this species into the nearby Swartkops estuary (Mellville-Smith & Baird, 1980). In Swartvlei Bay, postflexion larval *S. bleekeri* < 5 mm TL were present in the surf zone from November-May, with estuarine recruitment recorded from November-March (Whitfield, 1989b). Bennett (1989), working in the Palmiet and Kleinmond estuaries, also recorded a November-March recruitment period but his specimens (seine net samples) were larger (40-55 mm TL) than those entering the Swartvlei or Swartkops estuaries (plankton net samples). In the Knysna estuary, *S. bleekeri* < 50 mm TL were recorded in the seine net catches throughout the year with no discernable recruitment peak. This species is distributed throughout the Knysna and Swartvlei estuarine systems.

Heteromycteris capensis (Family: Soleidae)

Spawning by this species in False Bay was recorded throughout the year with a peak between October and February (Brownell, 1979). Evidence to support a protracted breeding season by *H. capensis* is provided by Beckley (1986) who found moderate numbers of larvae throughout the year in Algoa Bay. Postflexion larval *H. capensis* < 10 mm TL were present in the Swartvlei Bay surf zone from September-May, with a peak in abundance during March. Recruitment into the Swartvlei estuary was recorded between October and March (Whitfield, 1989b). In the Knysna estuary *H. capensis* 20-30 mm TL were captured between December and March. No specimens were captured in the upper reaches of either the Swartvlei or Knysna estuaries.

Pomadasys commersonnii (Family: Haemulidae)

Spawning by this species in Natal waters takes place mainly between August and December (Wallace, 1975a), with estuarine recruitment first occurring between 20 mm and 30 mm TL (Wallace & van der Elst, 1975). Migration of < 50 mm TL specimens into Natal estuaries occurs from September to December, and in the Knysna estuary recruitment of this size group peaked in October.

P. commersonnii attain approximately 200 mm TL in their first year (Wallace & van der Elst, 1975), at which stage they return to the sea (Day *et al*., 1981). Adult spotted grunter are common in southern African estuaries (Marais & Baird, 1980), with post-spawners returning in large numbers to the St Lucia system from August onwards (Wallace, 1975a).

Pomadasys olivaceum (Family: Haemulidae)

The juveniles of this species occur mainly in shallow coastal waters, where they congregate in large shoals (Romer, 1990). The spawning season is prolonged, with *P. olivaceum* fry of < 50 mm TL occurring throughout the year in Algoa Bay (Lasiak, 1983a) and inshore reefs along the Natal coast (Joubert, 1981). This size group was most abundant in the lower and middle reaches of the Knysna estuary during December, and no specimens were captured between April and September. Stragglers have been recorded from the upper reaches of both the Knysna and Swartvlei estuaries. In contrast, beam trawls off the mouth of the Swartkops estuary revealed that *P. olivaceum* < 60 mm TL comprised 76% of the total catch (Beckley, 1984b).

Pomatomus saltatrix (Family: Pomatomidae)

Although primarily a marine species in southern African waters, *P. saltatrix* juveniles do utilize estuarine nursery areas (Smale & Kok, 1983), and are occasionally recorded in the upper reaches of these systems (Whitfield, 1986; this study). Spawning occurs in the Natal region during spring, with the pelagic larvae drifting passively southwards in the Agulhas Current (van der Elst, 1981). Juveniles (< 40 mm TL) entered the Knysna estuary between September and December. In southwestern Cape estuaries, recruitment of 40-120 mm TL *P. saltatrix* was recorded between December and March (Bennett, 1989).

Terapon jarbua (Family: Teraponidae)

This tropical Indo-Pacific species is normally absent from southern Cape estuaries but a small population finds refuge in a warm water power station outlet in the Knysna estuary. *T. jarbua* spawns in Natal waters during the summer (Day *et al*., 1981) with juveniles 10-30 mm TL entering adjacent estuaries between November and May (Wallace & van der Elst, 1975). In the Knysna estuary, specimens < 30 mm TL were recorded during March and April. Winter water temperatures, together with cold upwelling events during summer, probably limit the penetration of this species into southern Cape waters. No *T. jarbua* were captured in the Swartvlei estuary.

Valamugil buchanani (Family: Mugilidae)

According to Wallace (1975a), this species spawns between October and December in Natal waters, with recruitment of fry < 50 mm TL occurring mainly during the months February-July. *V. buchanani* 10-50 mm SL were captured in Natal and Transkei estuaries during summer and winter (Blaber & Whitfield, 1977). Immigration of juveniles < 40 mm TL into the Knysna estuary occurred mainly during March-June. This species remains in the lower reaches of both the Knysna and Swartvlei estuaries, and has not been recorded from the upper reaches of either system.

Hemiramphus far (Family: Hemiramphidae)

This species spawns during the summer (Smith, 1933; Wallace, 1975a), with the young first appearing in southern Cape estuaries during November and declining in numbers by March (Smith, *op. cit.*). A peak in 0 + juvenile (50-100 mm TL) numbers in the Knysna estuary was recorded during February, which corresponds closely to the January peak documented by Smith (1933). Juvenile *H. far* occurred in low numbers throughout the Knysna estuary. A few *H. far* were captured in the lower reaches of the Swartvlei estuary, where this species can be considered a marine straggler.

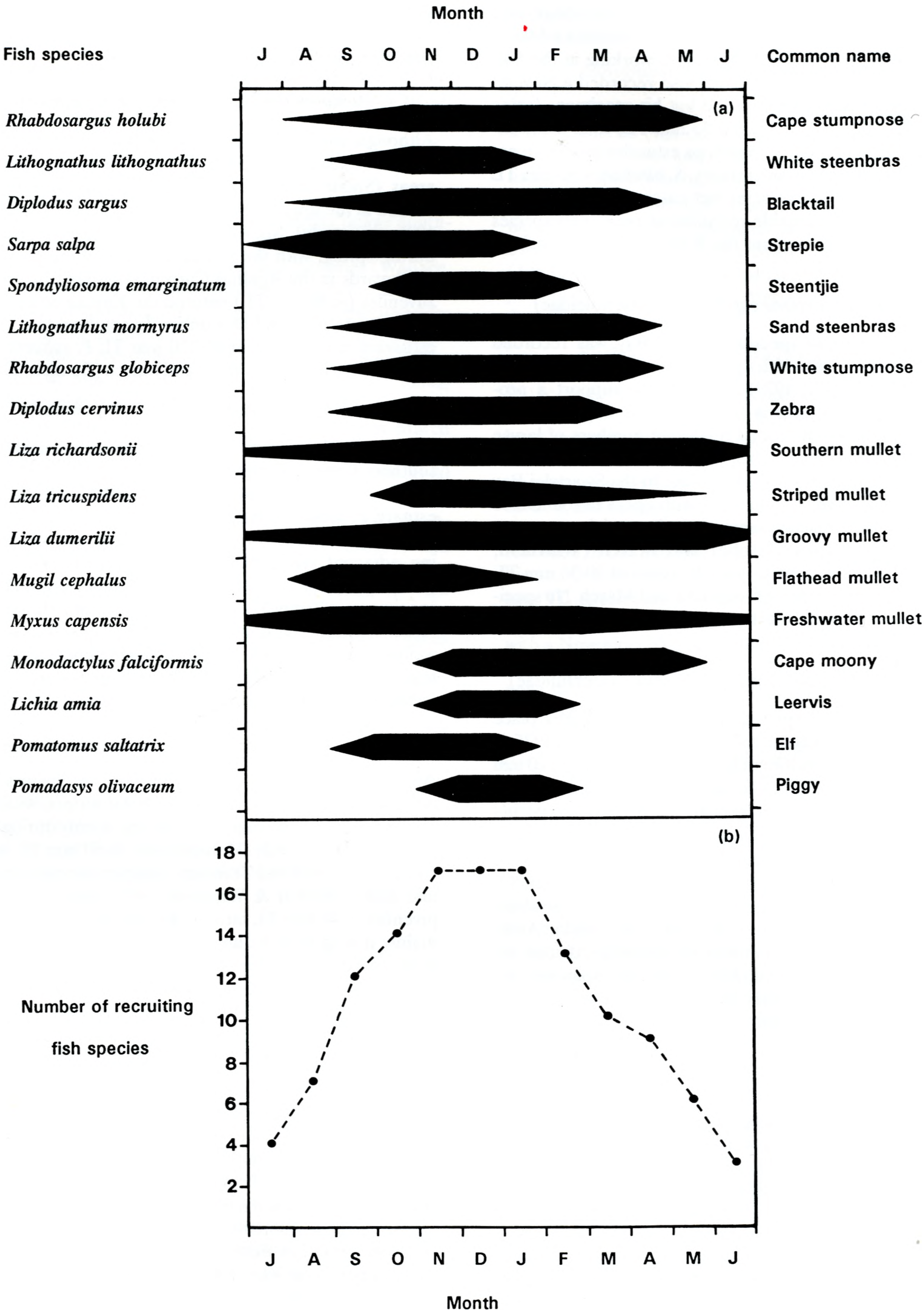

Figure 4. (a) Diagrammatic representation of juvenile recruitment of selected marine fish species into the Knysna and Swartvlei estuaries. (b) Monthly variation in the numbers of species entering these estuaries, as derived from bar representations shown in (a).

COMPARISONS BETWEEN PERMANENTLY OPEN AND SEASONALLY CLOSED ESTUARIES IN THE SOUTHERN AND SOUTHWESTERN CAPE

Numerous factors influence the abundance of marine fish in southern African estuaries (Marais, 1988). These include the ability of species to adjust to salinity and temperature fluctuations (Blaber, 1974b), predation (Blaber, 1973), whether an estuary is open or closed (Bennett *et al*., 1985), the occurrence and severity of floods (Marais, 1982), presence or absence of catchment dams (Plumstead, 1990), estuary size (Whitfield, 1983), turbidity (Cyrus & Blaber, 1987), latitude (Blaber, 1981), habitat variation (Blaber, 1978), and degradation as a result of pollution (Blaber *et al*., 1984).

Of these factors, the open/closed condition of an estuary is probably the major determinant of fish species diversity and abundance. Formation of a sand bar across the mouth of an estuary effectively blocks any further recruitment of juveniles, or emigration of sub-adults/adults back to the sea, thereby directly influencing the composition of the fish community. For example, Lenanton & Hodgkin (1985) found that the number of fish species in the temporarily open Beaufort estuary (Western Australia) more than doubled, when compared to the closed phase, due to juvenile recruitment of marine species into that system. Bennett (1989), working in the closed Bot River estuary, calculated that marine migrants numerically comprised only 1% and residents 99% of the fish fauna, whereas the two groups occurred in approximately equal abundance in the nearby permanently open Palmiet estuary. In contrast to the prolonged (several years) closed phase of the Bot River estuary, the Swartvlei system normally opens annually and the marine migrants are therefore well represented in this estuary (Kok & Whitfield, 1986). Although resident species such as *Gilchristella aestuaria* are abundant in the Knysna estuary, marine migrants dominate this system (Whitfield *et al*., 1989).

Comparisons between the Swartvlei and Knysna estuaries indicate that the CPUE of most marine migrants were higher in the latter system (Table 1). Apart from mouth condition, most of the factors (listed above) influencing fish abundance in the two estuaries were similar. We therefore suggest that the relatively higher densities of most species in the Knysna system may be attributed to the deep, permanently open mouth and strong marine influence. A similar conclusion was reached by Whitfield *et al*. (1989), who found that the species richness of fishes associated with *Zostera* beds in the Knysna estuary was more than twice that of Swartvlei estuary eelgrass beds.

The species composition, abundance and size distribution of marine fishes within southern African estuaries undergo seasonal variations that are directly related to migration patterns. Recruitment of most species into southern Cape estuaries reaches a peak during summer (Fig. 4), which coincides with maximum food resource availability and corresponds to the time when systems along this section of the coast are normally open to the sea (Fig. 3). The prolonged recruitment periods of most fish species into the estuaries (Fig. 4) provide a buffer against the variability in mouth opening and other short-term extremes in the aquatic environment, e.g. nearshore upwelling (Schumann *et al*., 1982). However, artificial winter opening of the Swartvlei mouth has occurred in the past and has generally led to the premature closure of the system, to the detriment of the juvenile marine fish recruitment. In addition, the larvae of several summer recruiting species are absent from the nearshore marine environment during winter (Whitfield, 1989d). Loss of the 'head' of water accumulated during the winter rains effectively reduces the chances of a summer opening, thereby denying certain fish species access to estuarine nursery areas.

Prolonged closure of an estuary, in association with dilution of lagoonal waters from catchment rivers, can lead to osmoregulatory stress for resident marine fish species. In October 1981, after four years of isolation from the sea, the maximum salinity in the Bot River estuary decreased to 3 g kg^{-1} resulting in a mass mortality of nine marine species (Bennett, 1985). Salinities in the Swartvlei estuary seldom decline below 10 g kg^{-1} (Kok & Whitfield, 1986), thus avoiding salinities at which extensive fish kills are likely to occur (Whitfield *et al*., 1981).

There are benefits to those juvenile fish which enter estuaries that subsequently close. The nursery area available to foraging fishes in the Swartvlei and Bot estuaries increases considerably during the lagoonal phase due to elevated water levels inundating intertidal and supratidal habitats (Kok & Whitfield, 1986). These shallow littoral habitats are often inaccessible to large predatory fishes, thereby enhancing their nursery function. Breaching of closed estuaries results in a decline in the volume and area of the aquatic environment, together with a slump in aquatic plant and invertebrate food resources (Branch *et al*., 1985). In contrast, permanently open systems such as the Knysna estuary offer a more predictable nursery area, which fluctuates in depth and area according to the tidal regime.

ACKNOWLEDGEMENTS

We thank the following people who have contributed to the production of this paper; Richard Barnard and Koos Wagner for assistance in the field and laboratory, Dave Voorvelt and Elaine Grant for the fish line drawings used to illustrate the bar graphs, Ian Russell who supplied recent Swartvlei mouth phase data, Marion Baxter for typesetting the manuscript, and Phil Heemstra for his very helpful editorial comments. The guidance and support of John Wallace in this research programme is gratefully acknowledged.

This work was financed directly or indirectly by a variety of organizations during the different stages of its development. They include the Port Elizabeth Museum, J.L.B. Smith Institute of Ichthyology, Institute for Freshwater Studies, and Estuaries Special Programme of the Foundation for Research Development.

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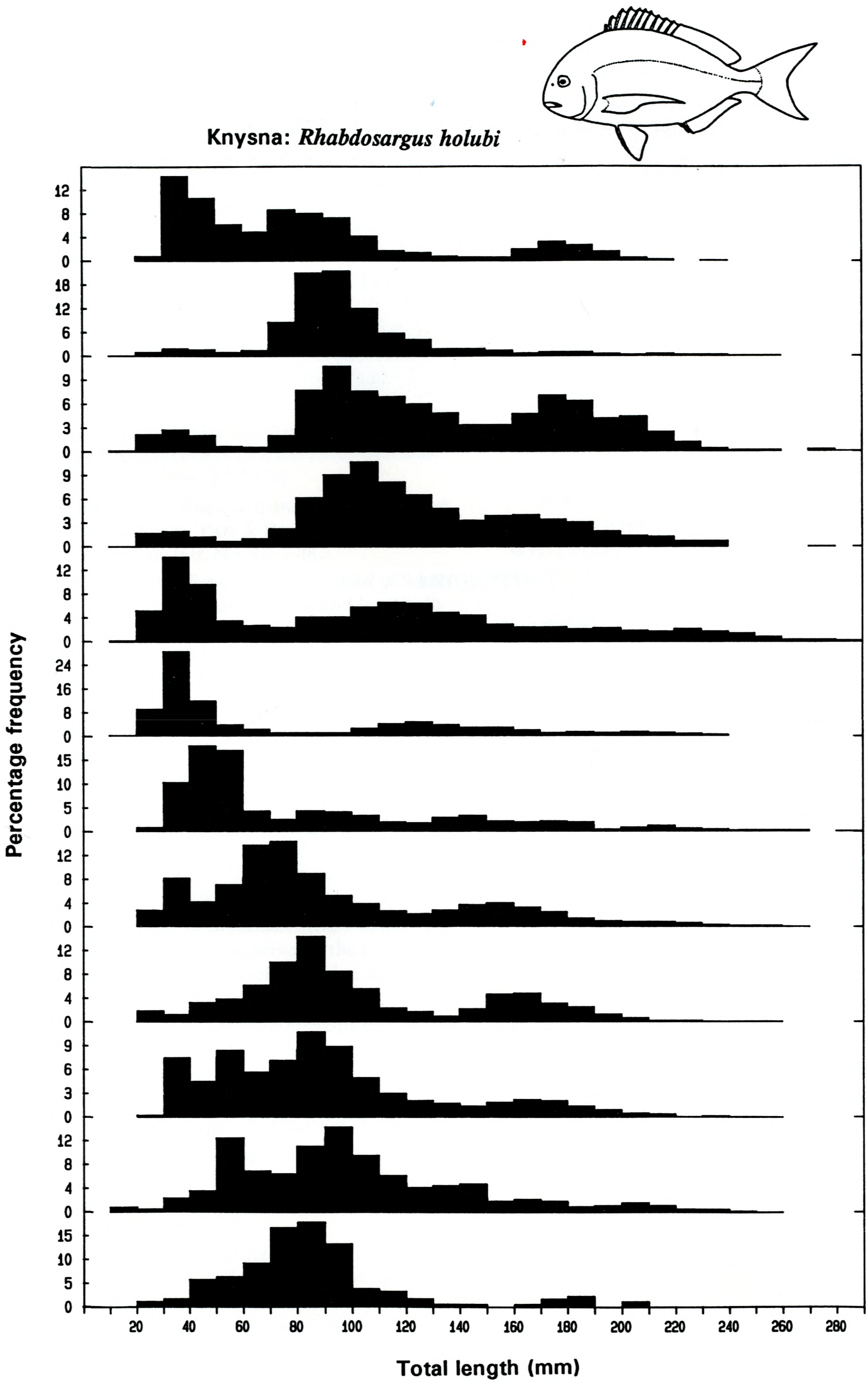
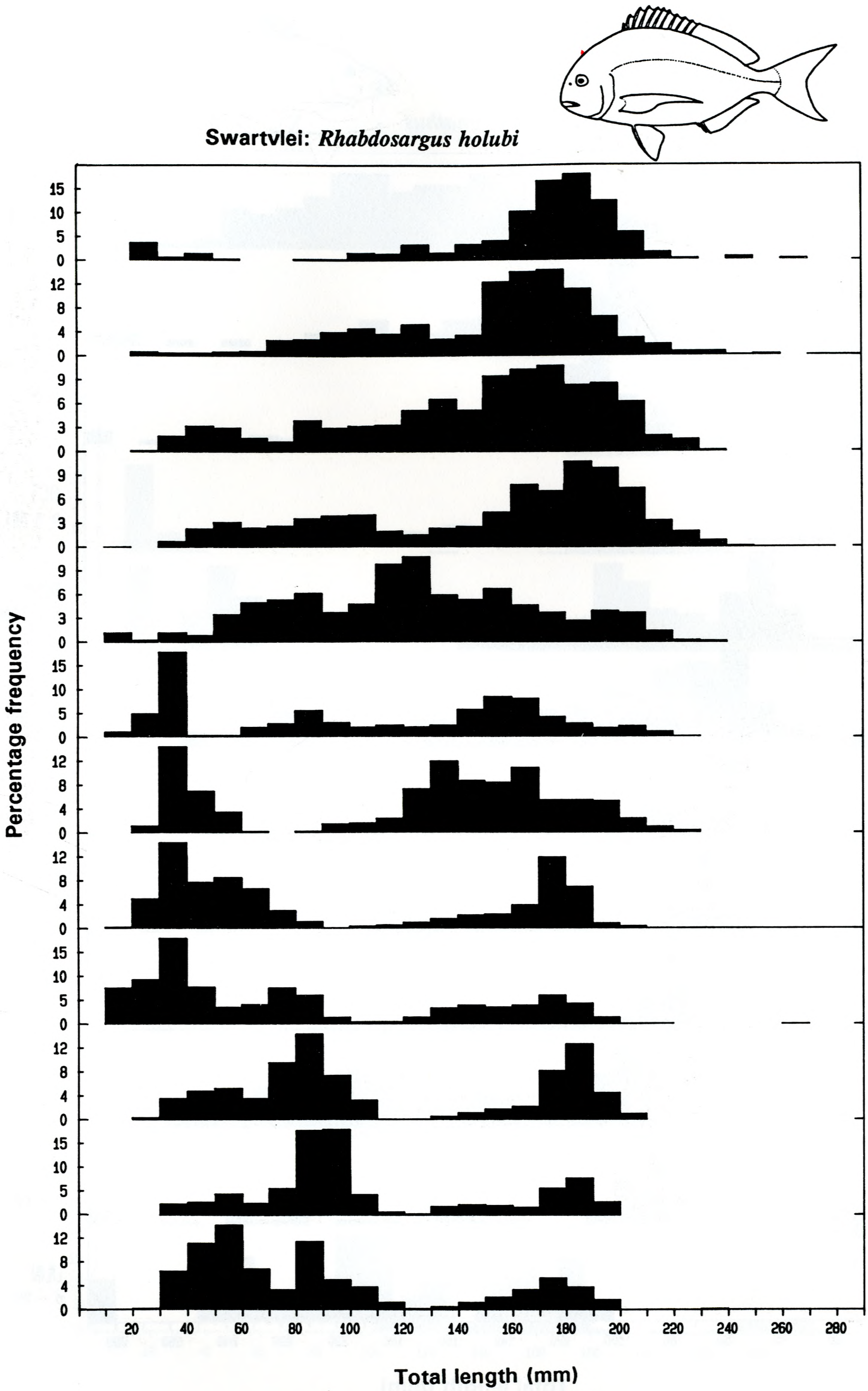
APPENDIX 1

(Bar Graphs 1 - 22)

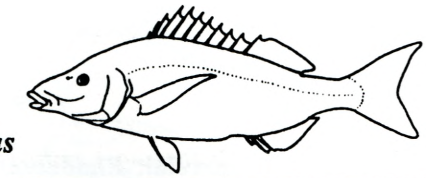


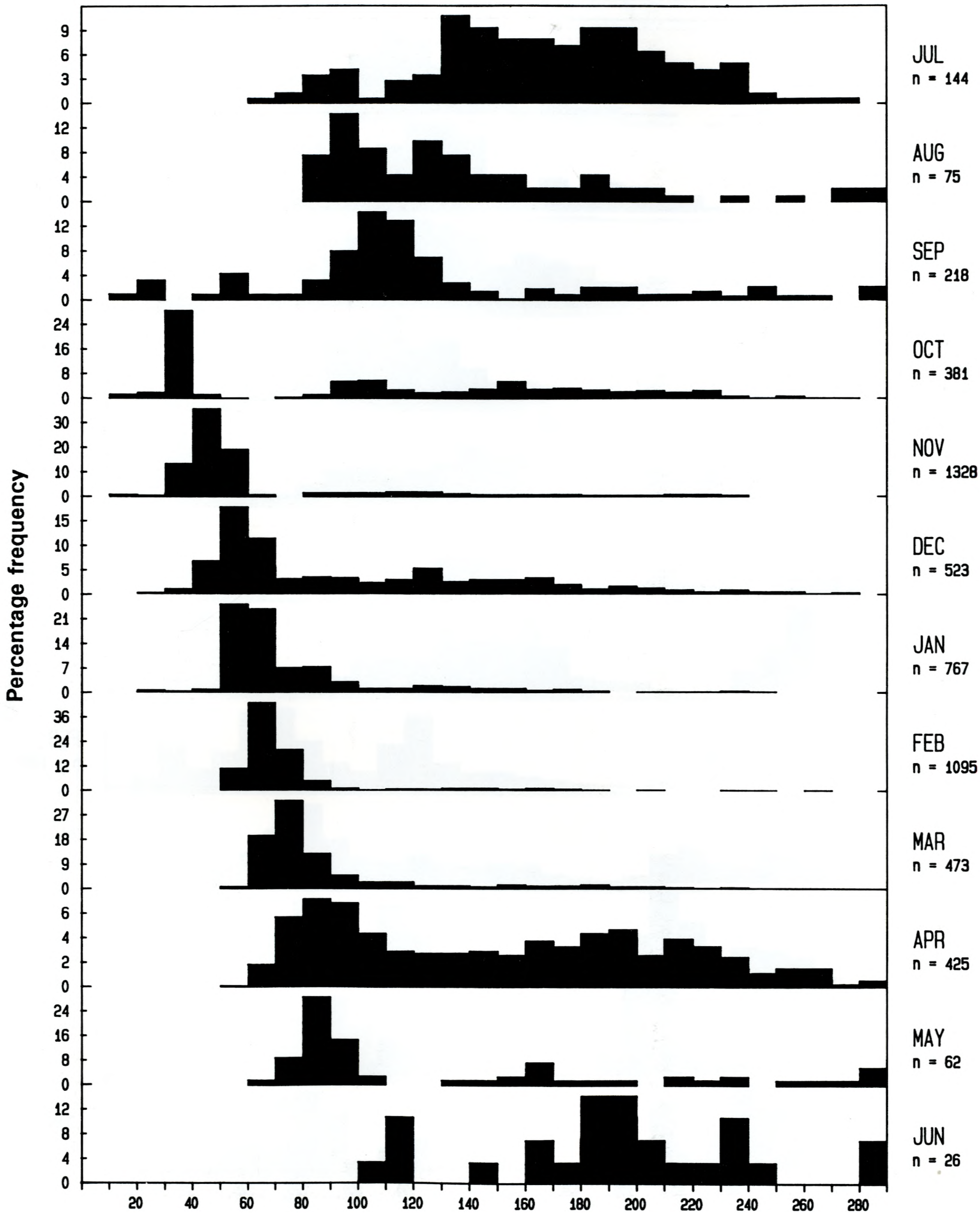
Bar Graph 1. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Rhabdosargus holubi* in the Knysna estuary (n = number of fish in sample).



Bar Graph 2. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Rhadosargus holubi* in the Swartvlei estuary (n = number of fish in the sample).

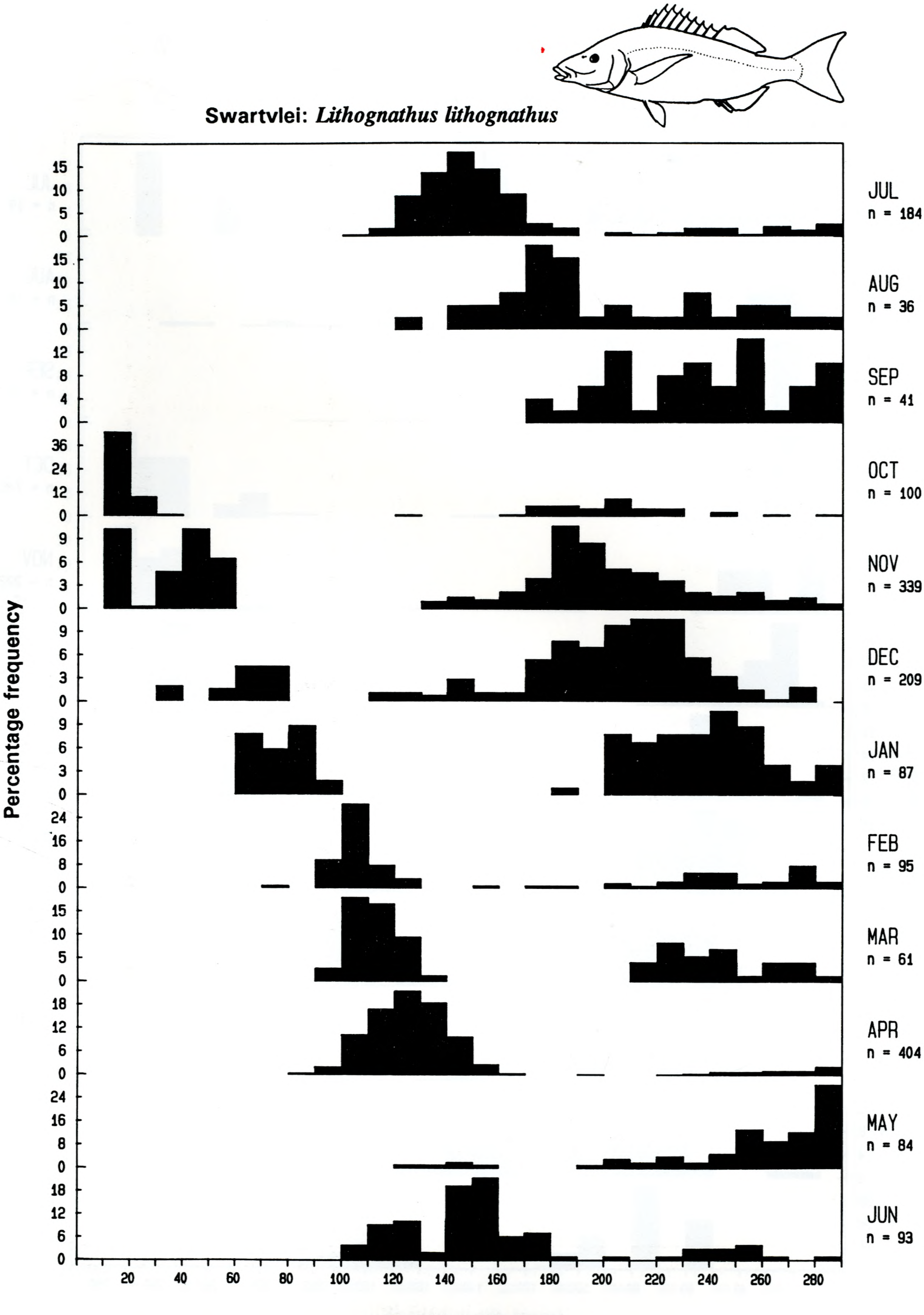
Knysna: *Lithognathus lithognathus*



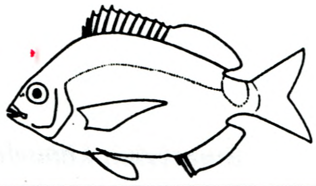


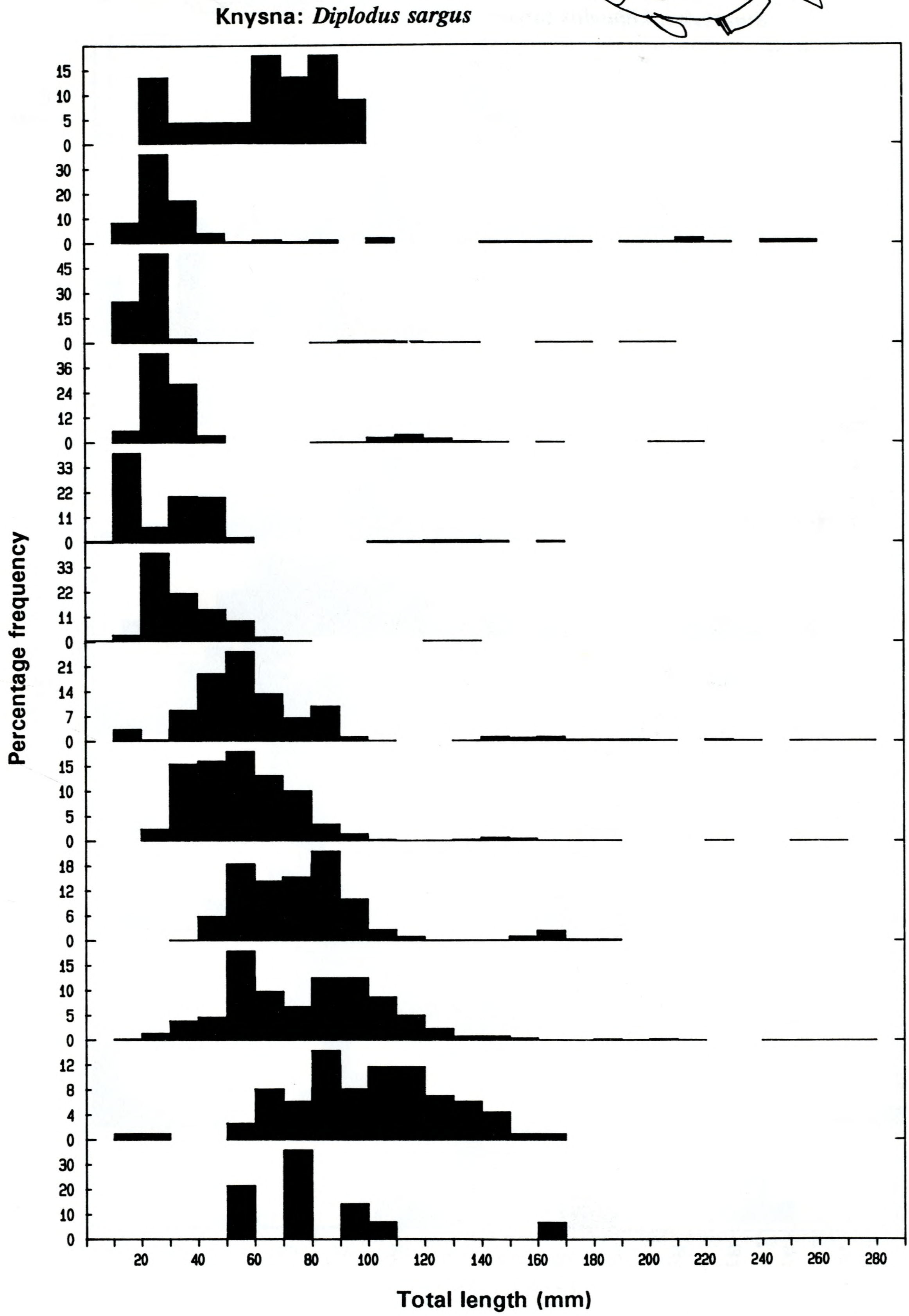
Bar Graph 3. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Lithognathus lithognathus* in the Knysna estuary (n = number of fish in the sample).

Swartvlei: *Lithognathus lithognathus*



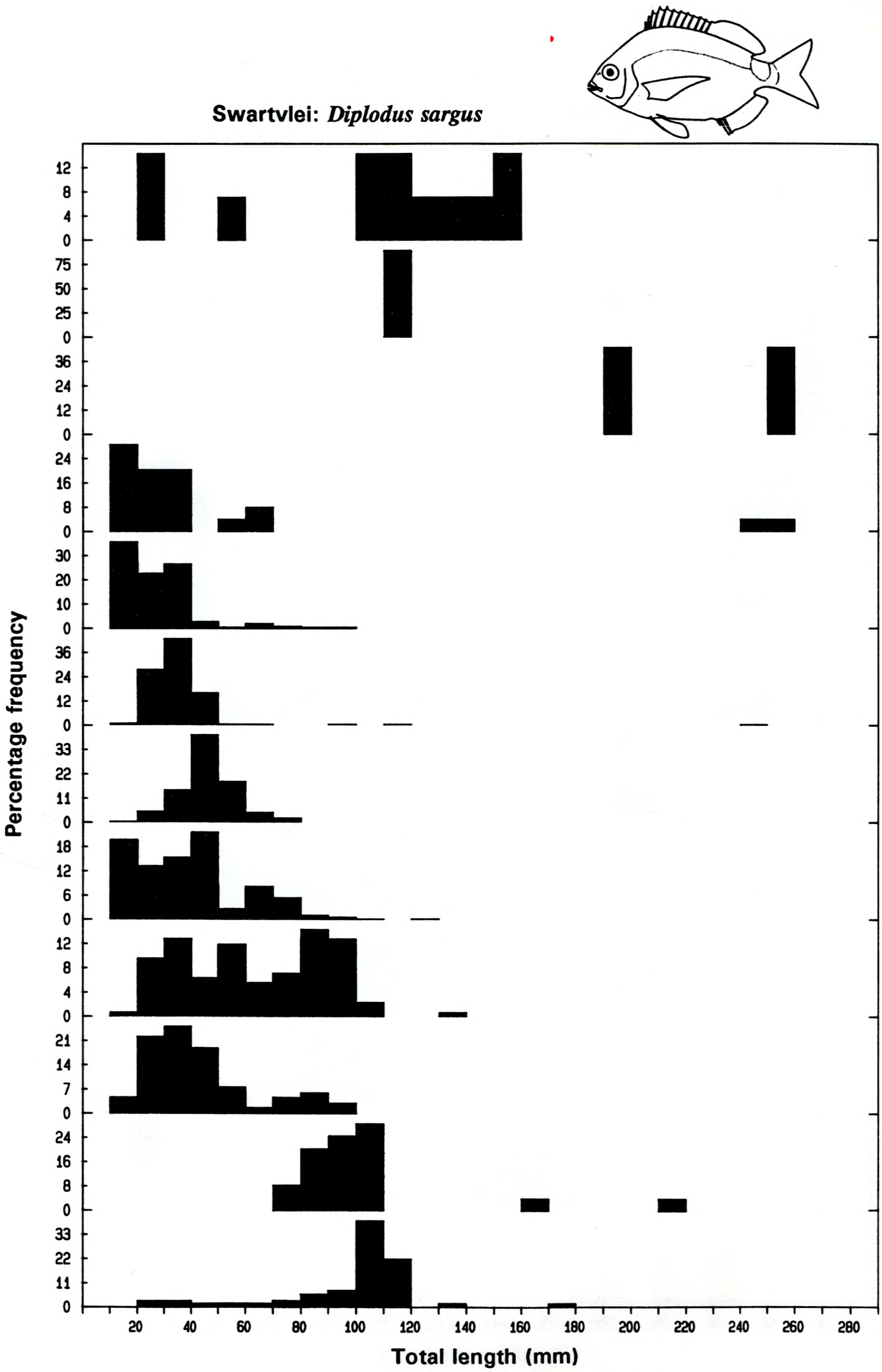
Bar Graph 4. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Lithognathus lithognathus* in the Swartvlei estuary (n = number of fish in the sample).



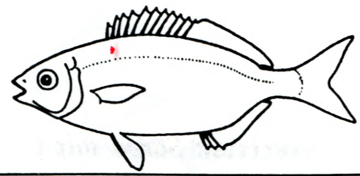


Bar Graph 5. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Diplodus sargus* in the Knysna estuary (n = number of fish in the sample).

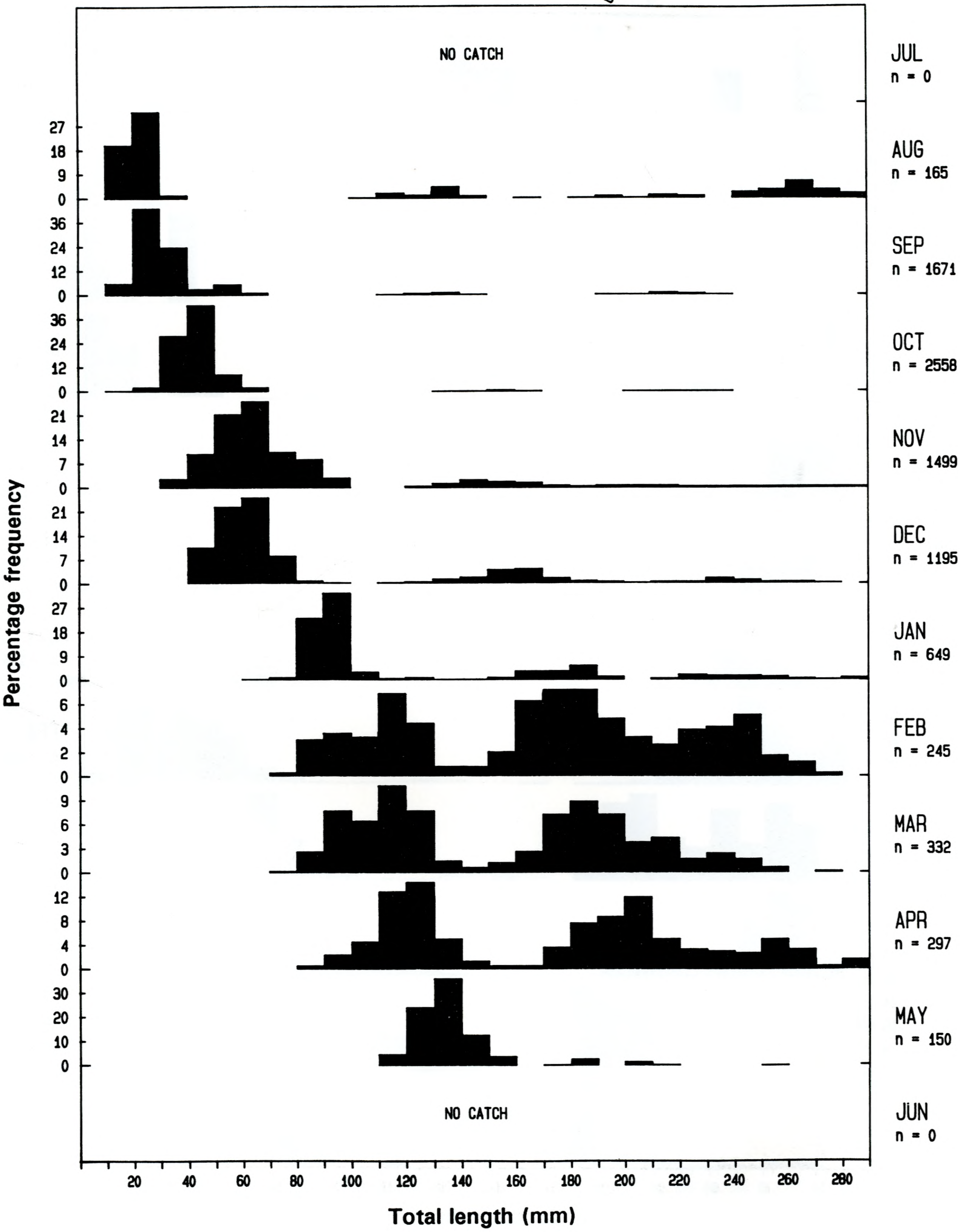
Swartvlei: *Diplodus sargus*



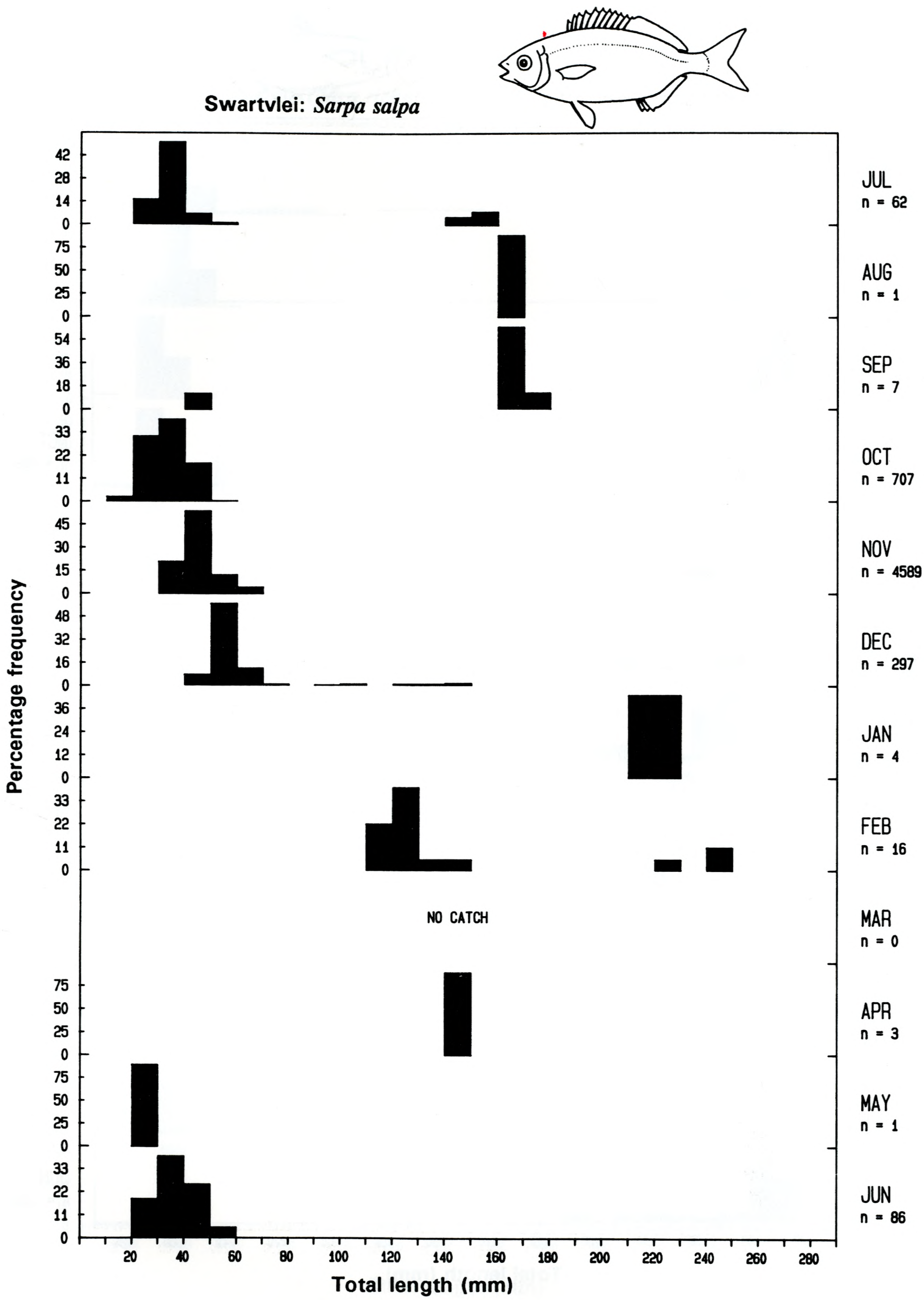
Bar Graph 6. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Diplodus sargus* in the Swartvlei estuary (n = number of fish in the sample).



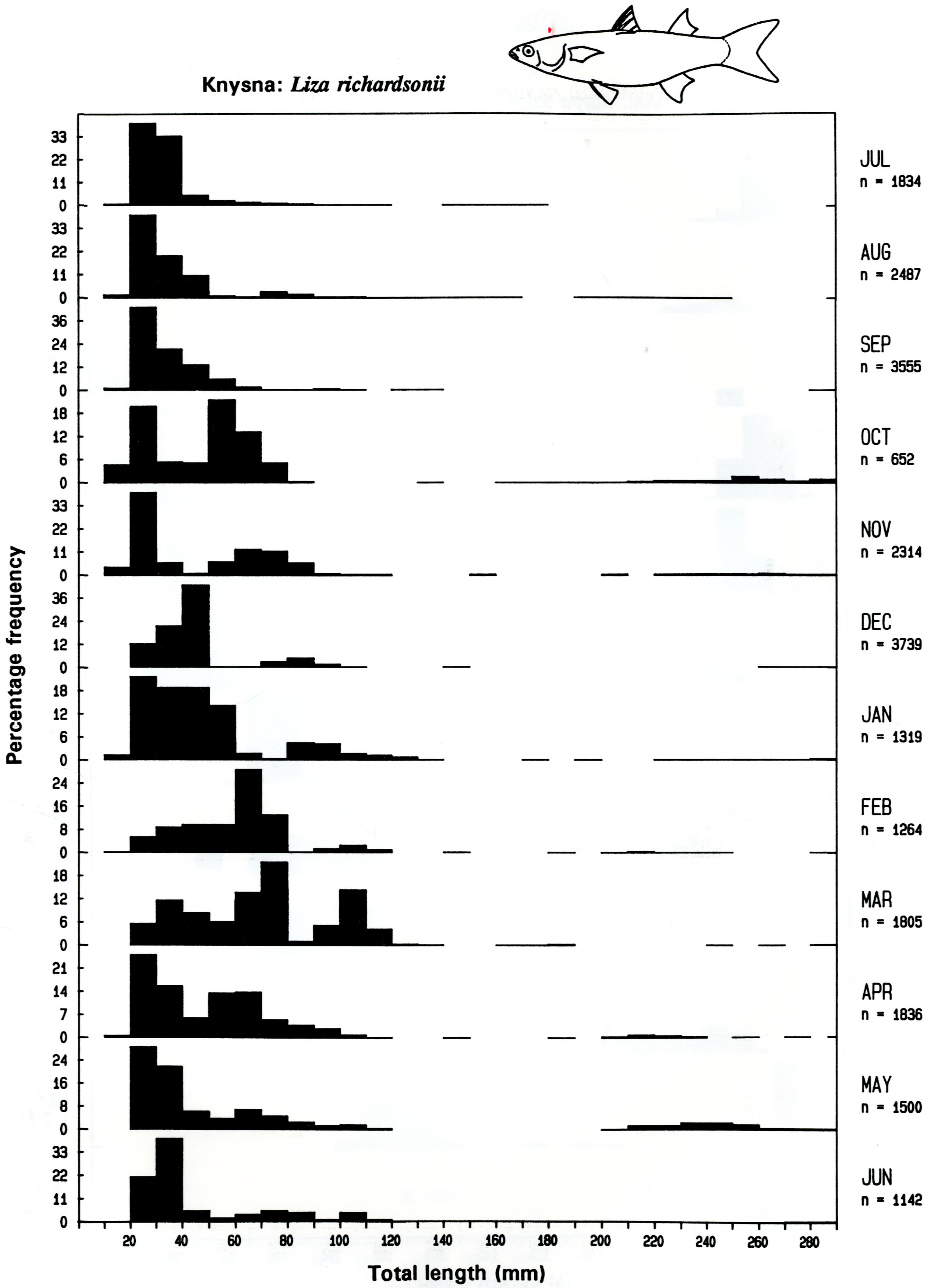
Knysna: *Sarpa salpa*



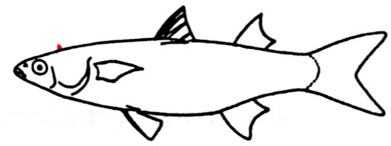
Bar Graph 7. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Sarpa salpa* in the Knysna estuary (n = number of fish in the sample).



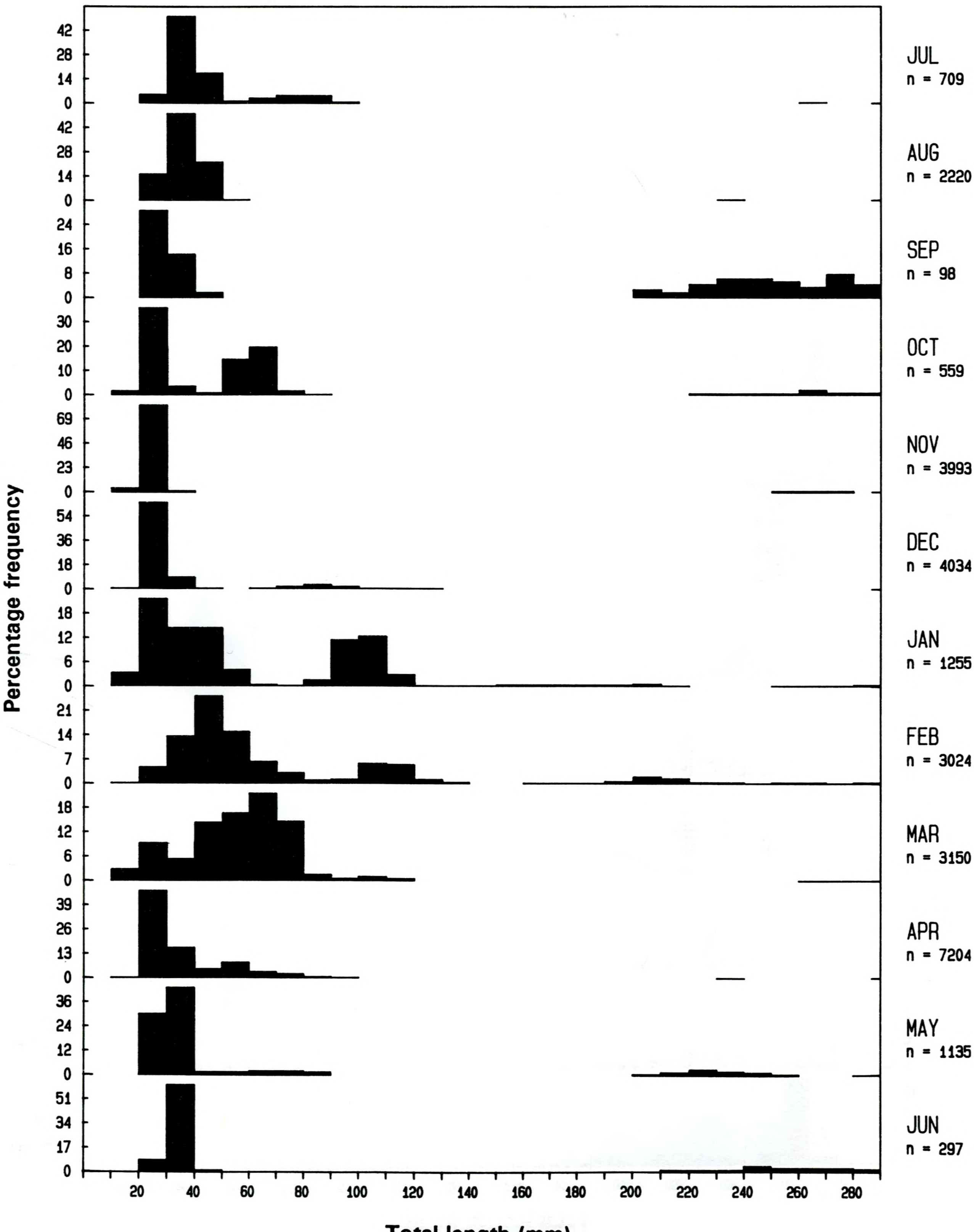
Bar Graph 8. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Sarpa salpa* in the Swartvlei estuary (n = number of fish in the sample).



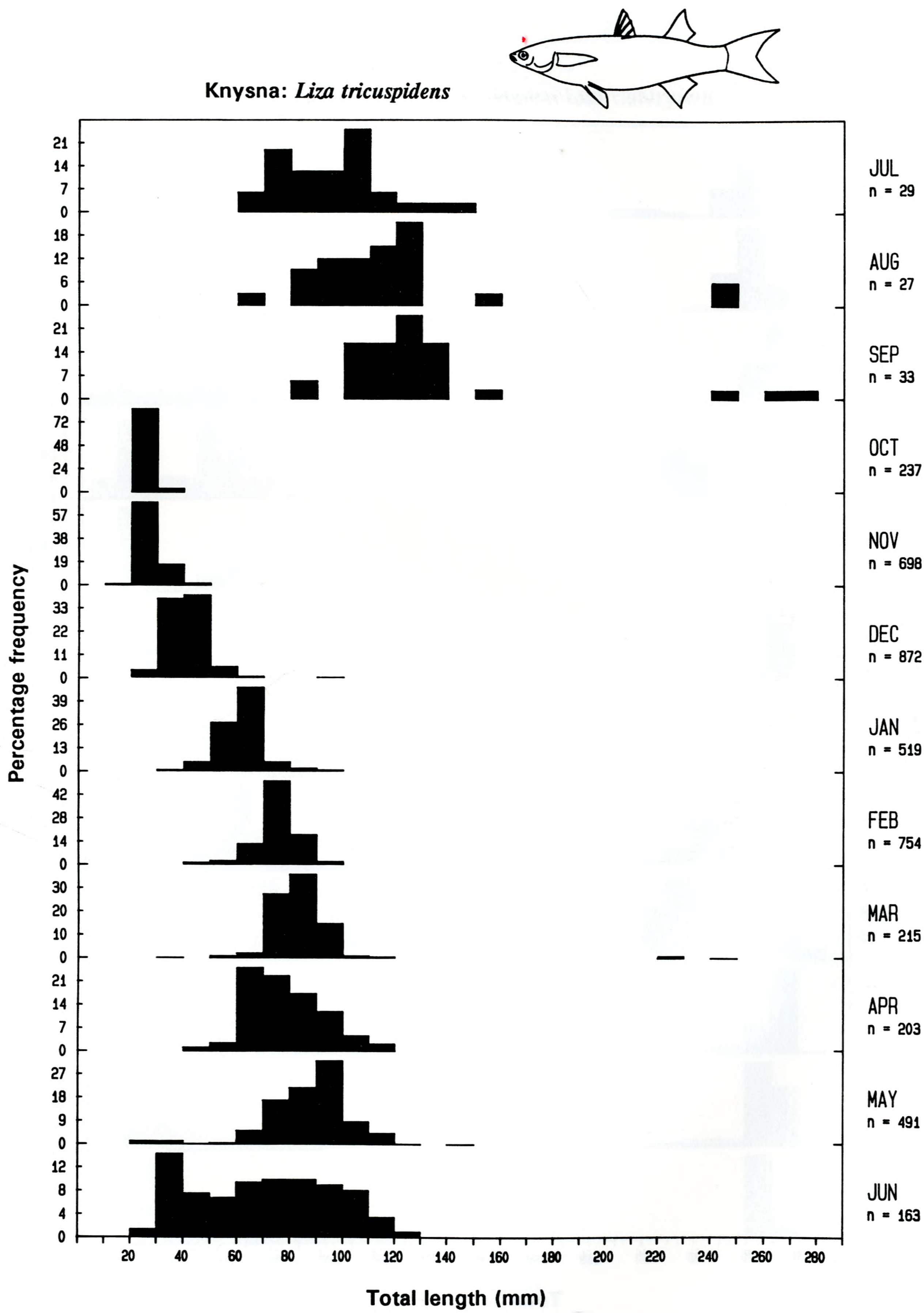
Bar Graph 9. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Liza richardsonii* in the Knysna estuary (n = number of fish in the sample).



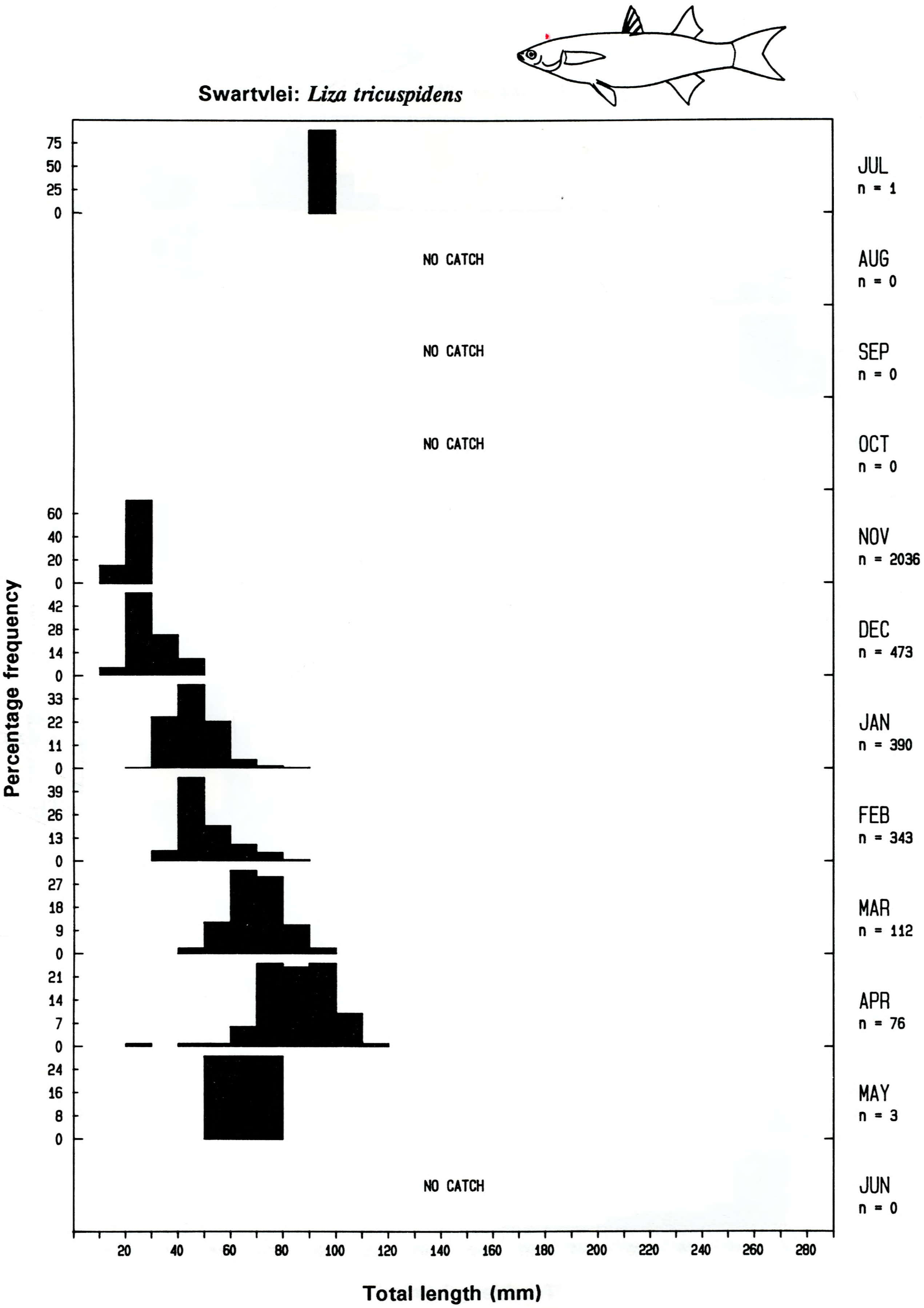
Swartvlei: *Liza richardsonii*



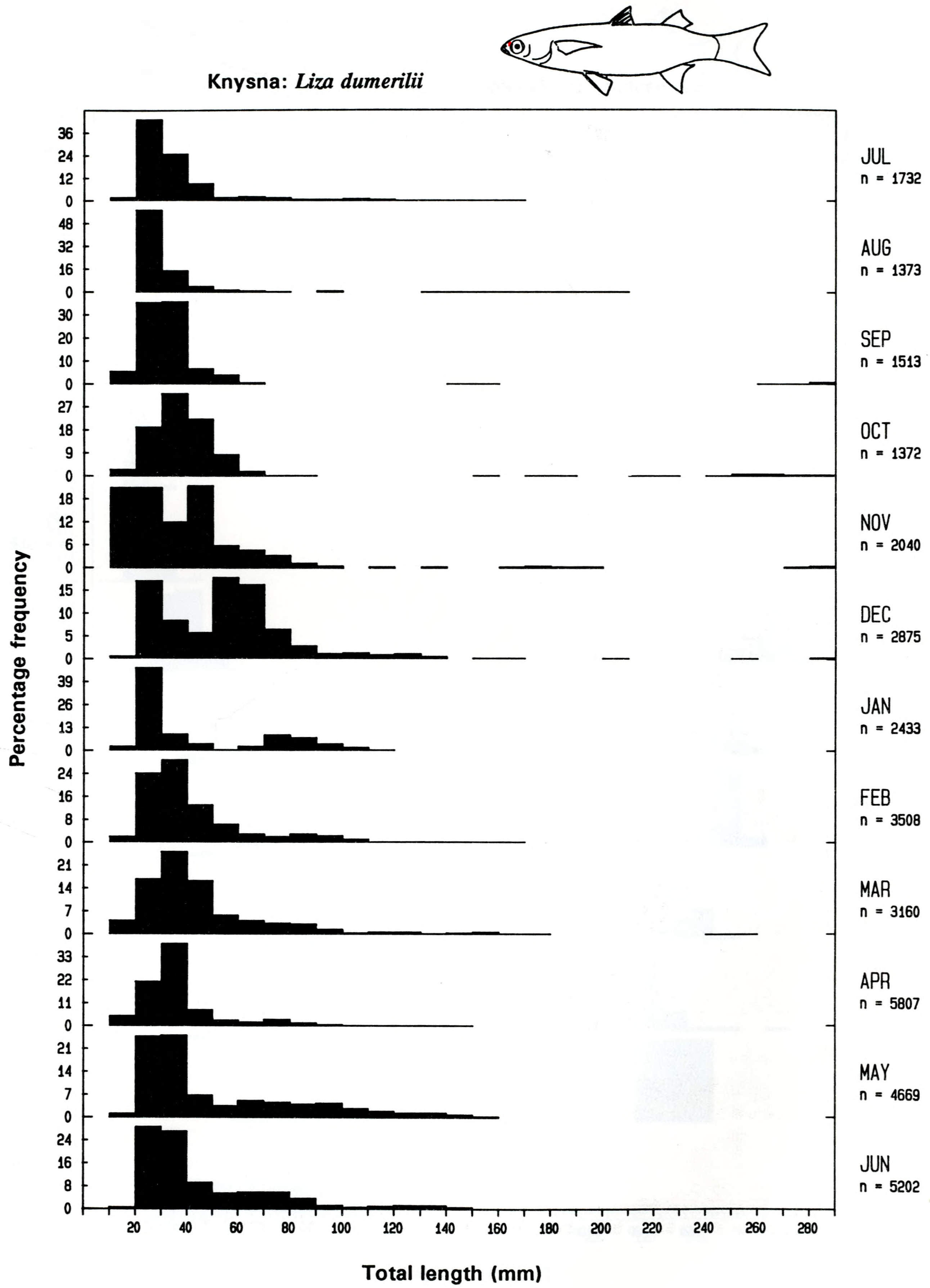
Bar Graph 10. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Liza richardsonii* in the Swartvlei estuary (n = number of fish in the sample).



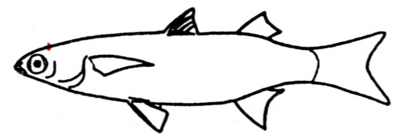
Bar Graph 11. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Liza tricuspidens* in the Knysna estuary (n = number of fish in the smaple).



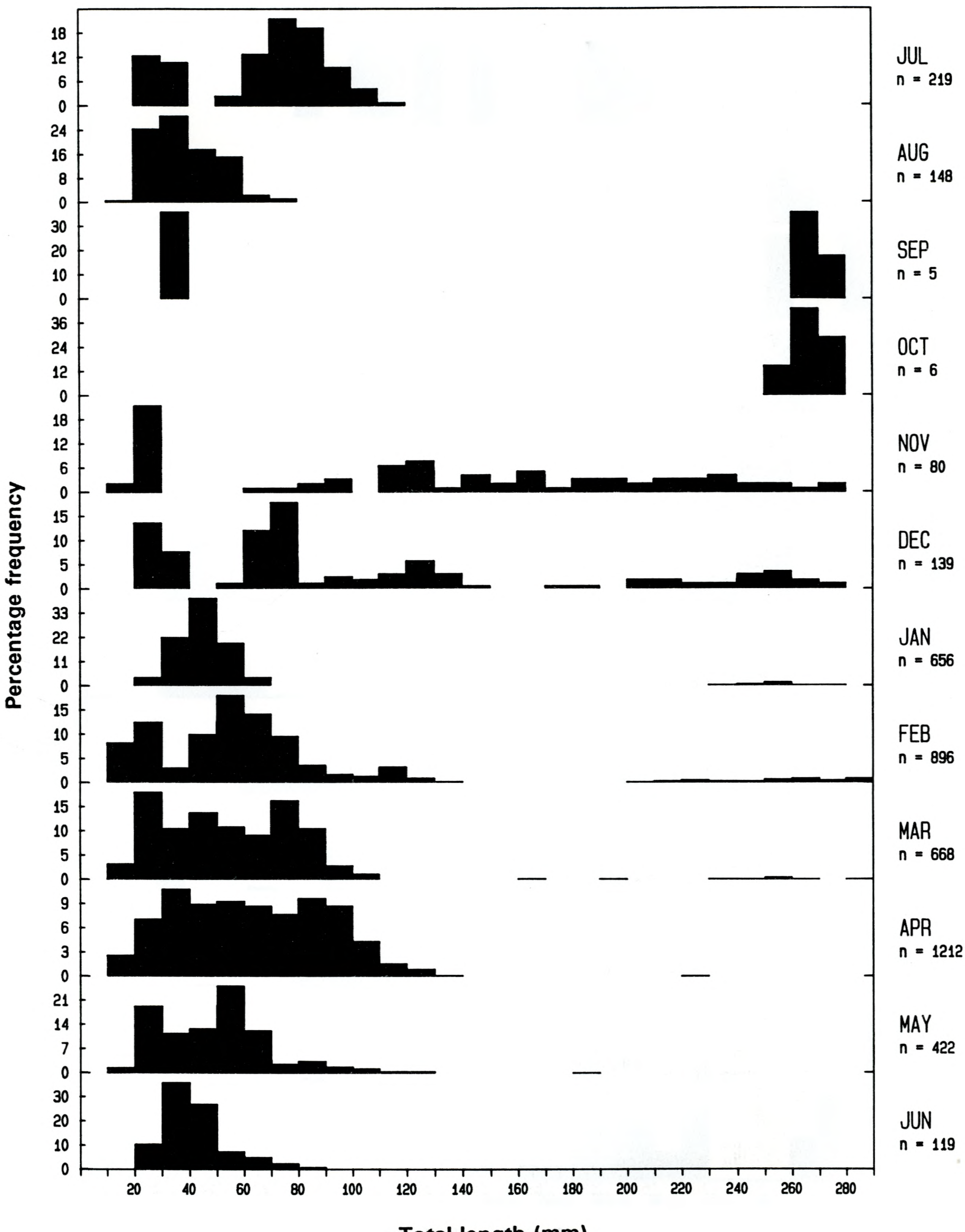
Bar Graph 12. Percentage length frequency distribution (1978- 1980 data combined) of juvenile *Liza tricuspidens* in the Swartvlei estuary (n = number of fish in the sample).



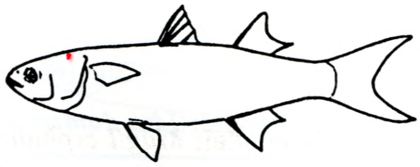
Bar Graph 13. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Liza dumerilii* in the Knysna estuary (n = number of fish in the sample).



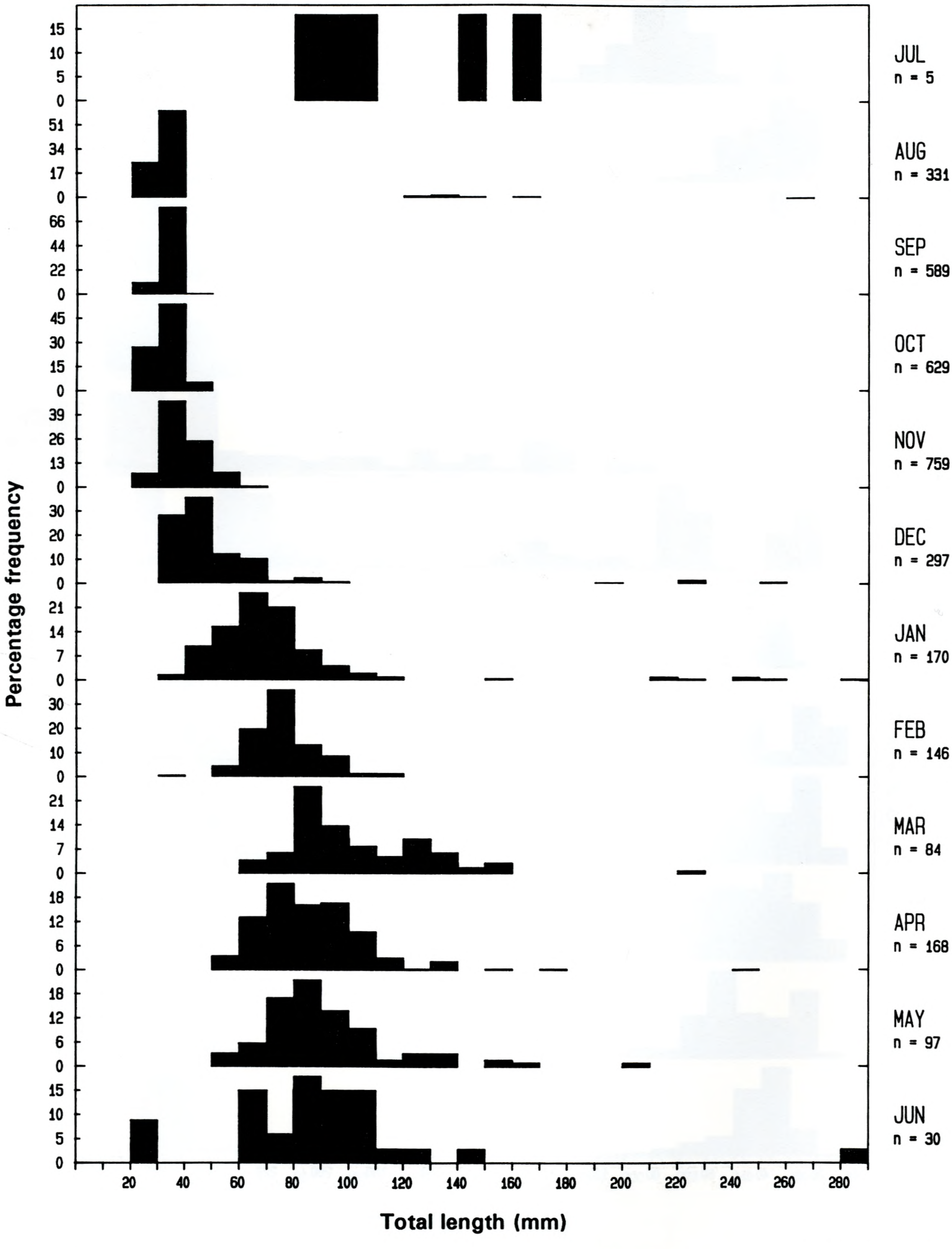
Swartvlei: *Liza dumerilii*



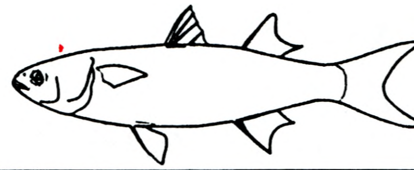
Bar Graph 14. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Liza dumerilii* in the Swartvlei estuary (n = number of fish in the sample).

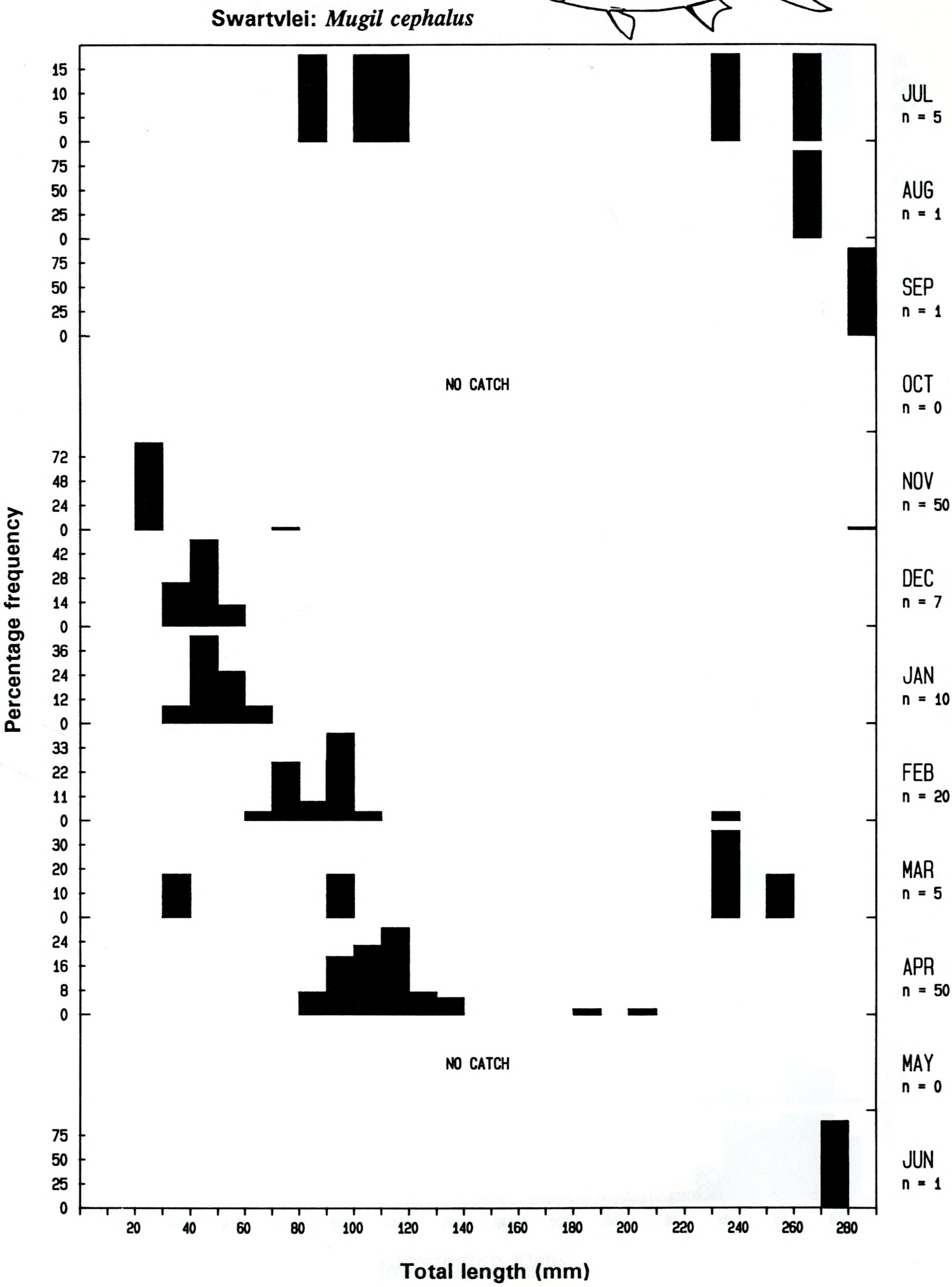


Knysna: *Mugil cephalus*



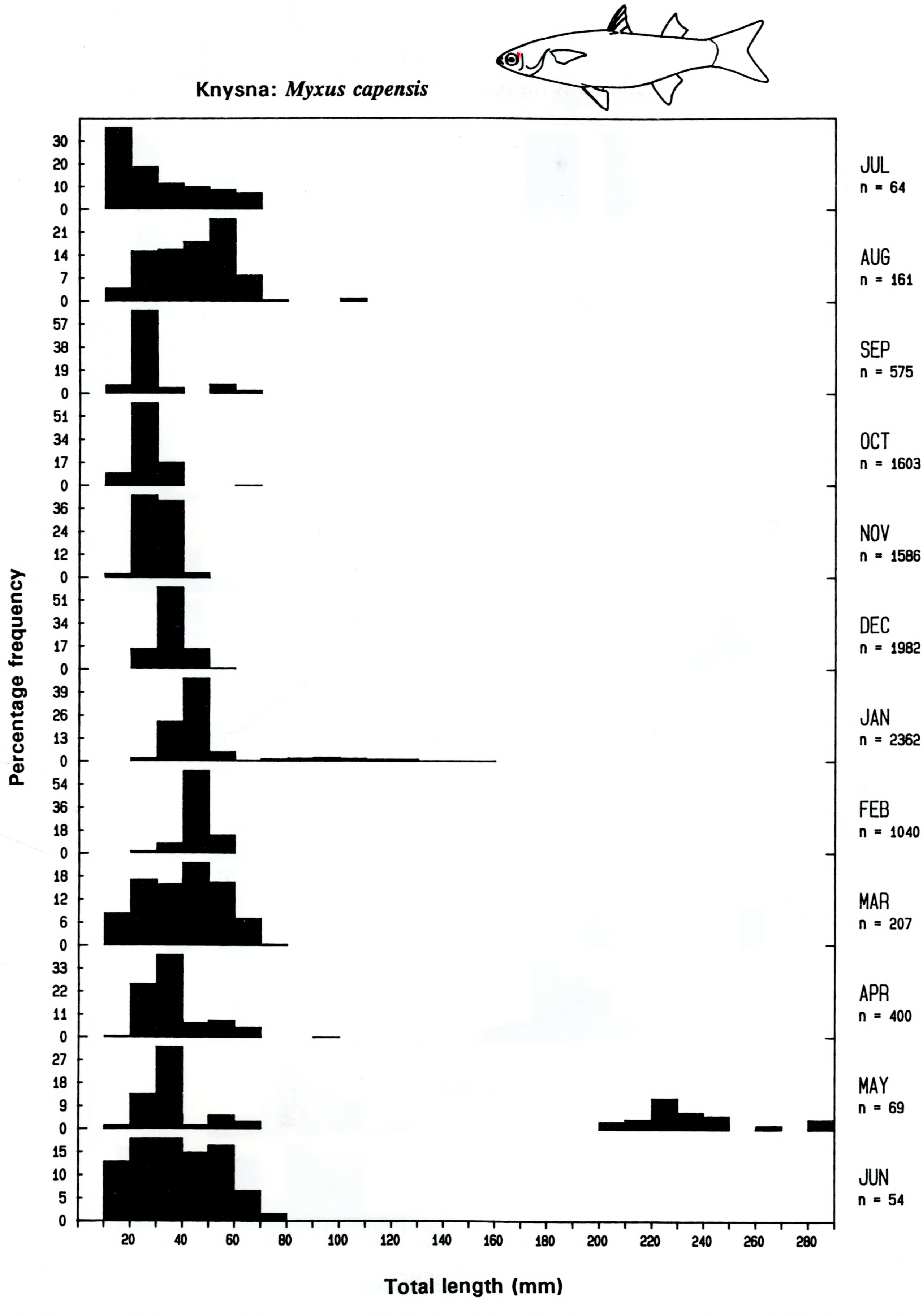
Bar Graph 15. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Mugil cephalus* in the Knysna estuary (n = number of fish in the sample).





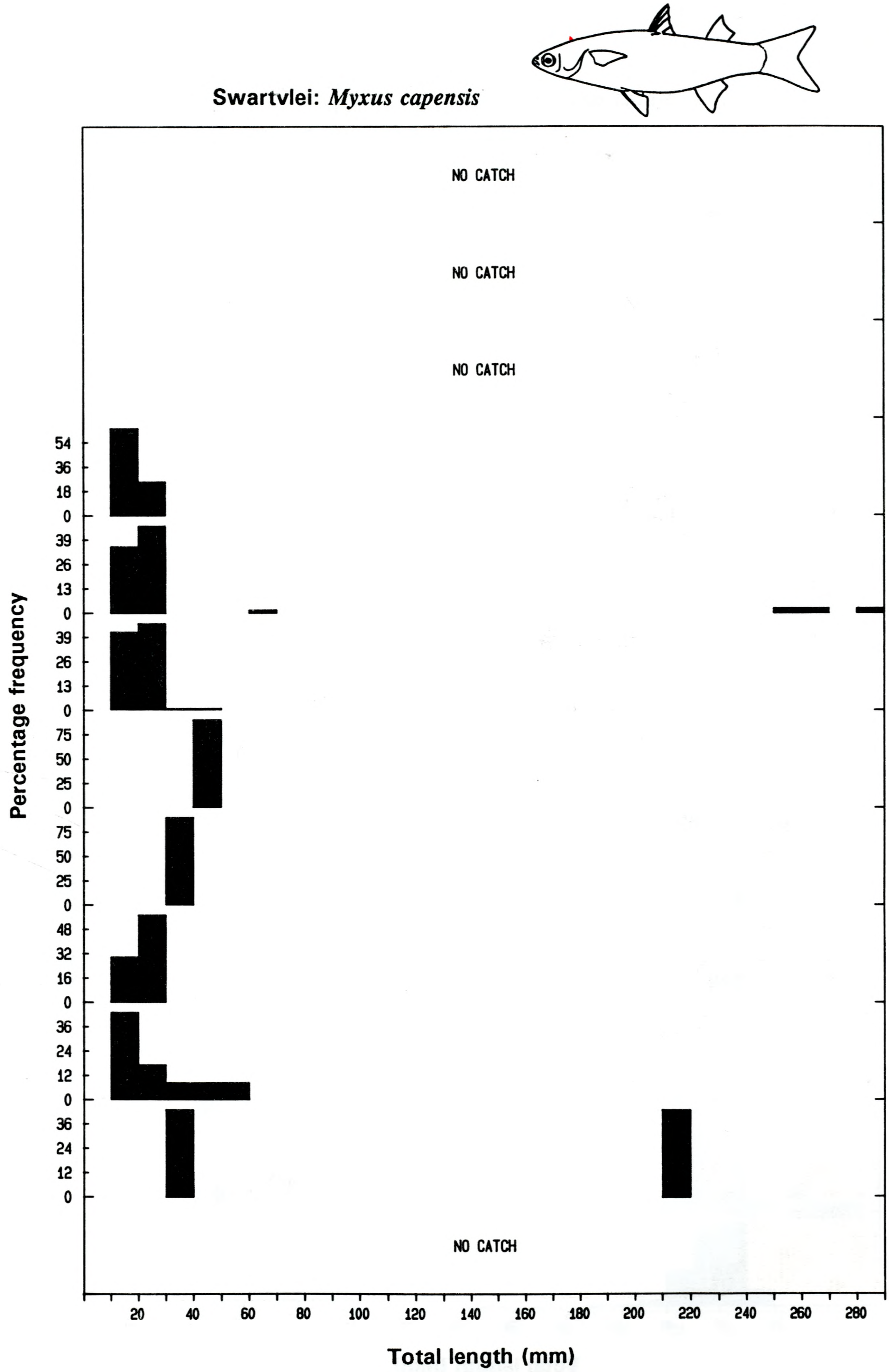
Bar Graph 16. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Mugil cephalus* in the Knysna estuary (n = number of fish in the sample).

Knysna: *Myxus capensis*

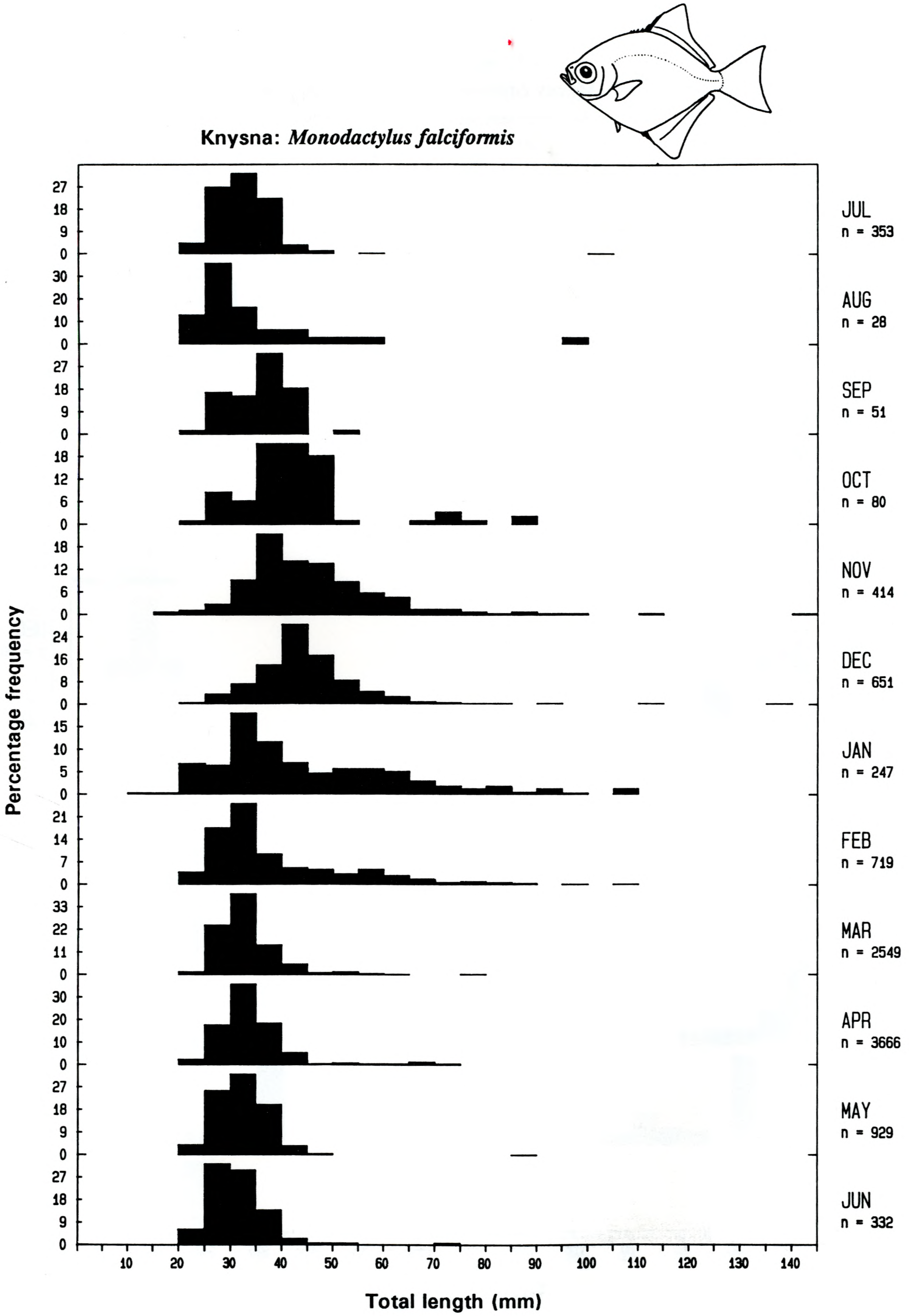


Bar Graph 17. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Myxus capensis* in the Knysna estuary (n = number of fish in the sample).

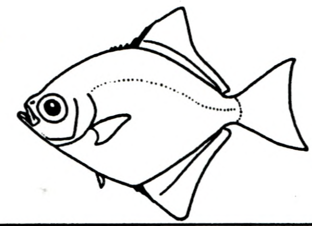
Swartvlei: ***Myxus capensis***



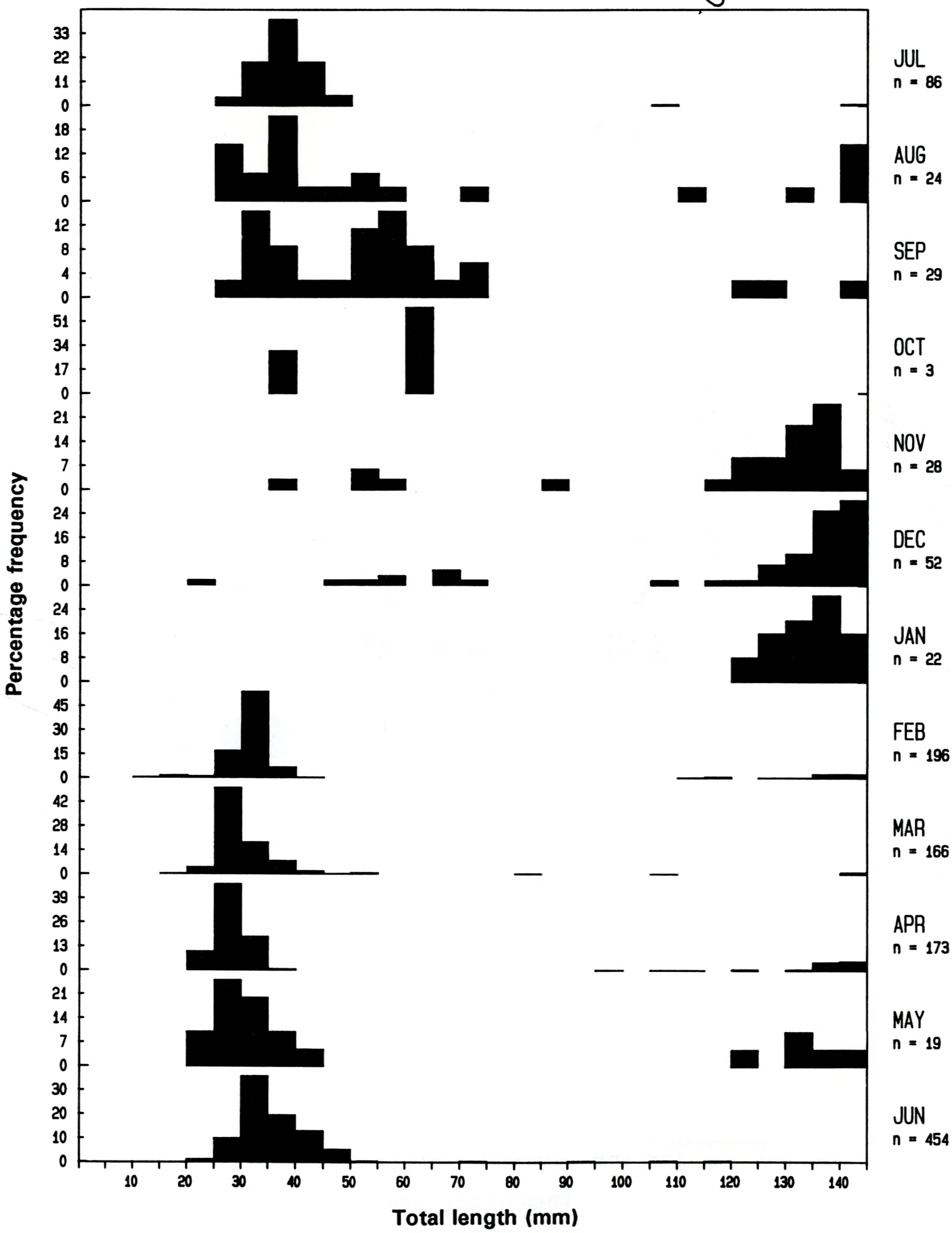
Bar Graph 18. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Myxus capensis* in the Swartvlei estuary (n = number of fish in the sample).



Bar Graph 19. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Monodactylus falciformis* in the Knysna estuary (n = number of fish in the sample).

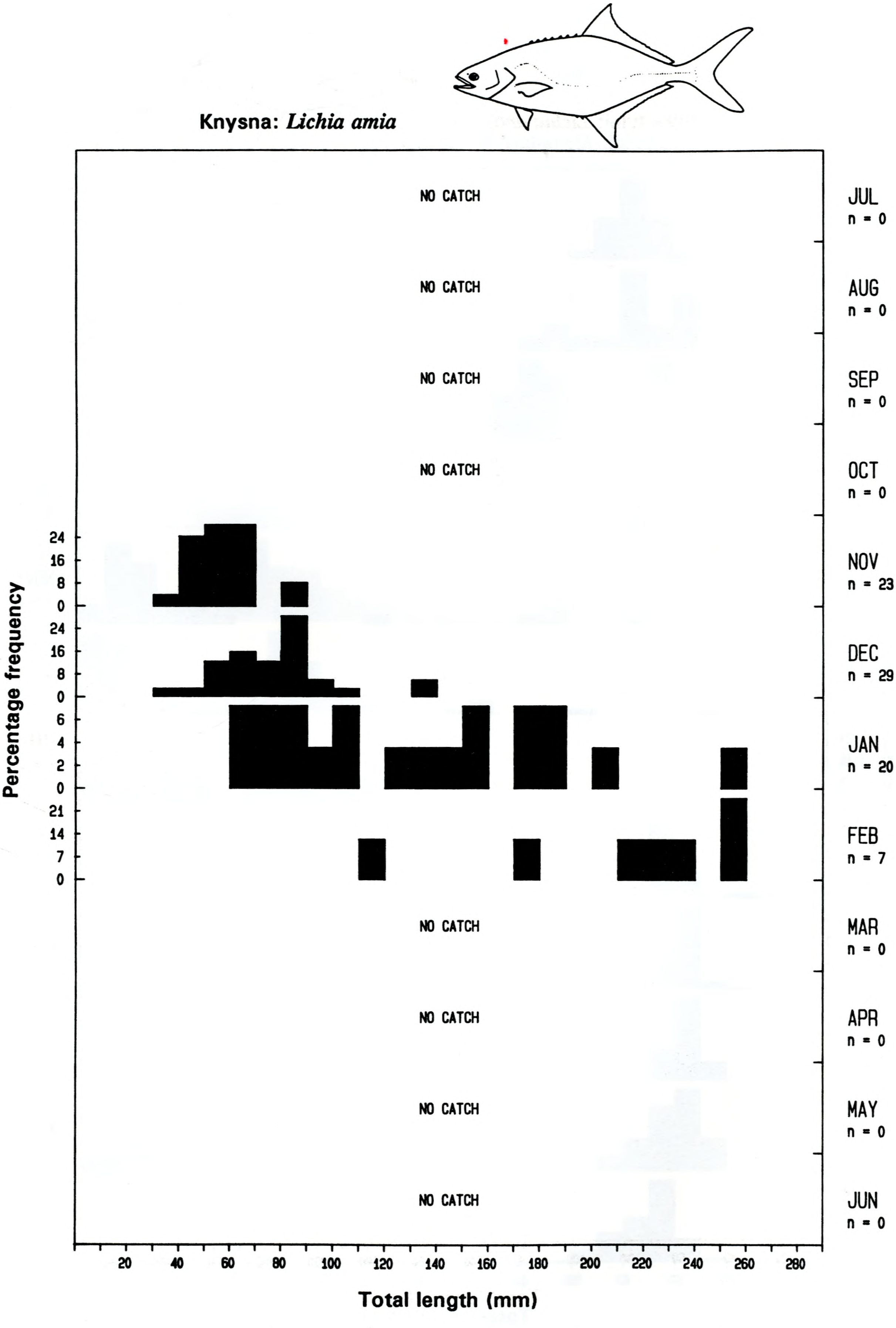


Swartvlei: ***Monodactylus falciformis***

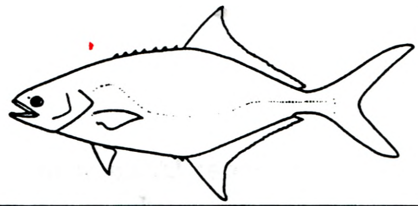


Bar Graph 20. Percentage length frequency distribution (1978-1980 data combined) of juvenile ***Monodactylus falciformis*** **in the Swartvlei estuary (n = number of fish in the sample).**

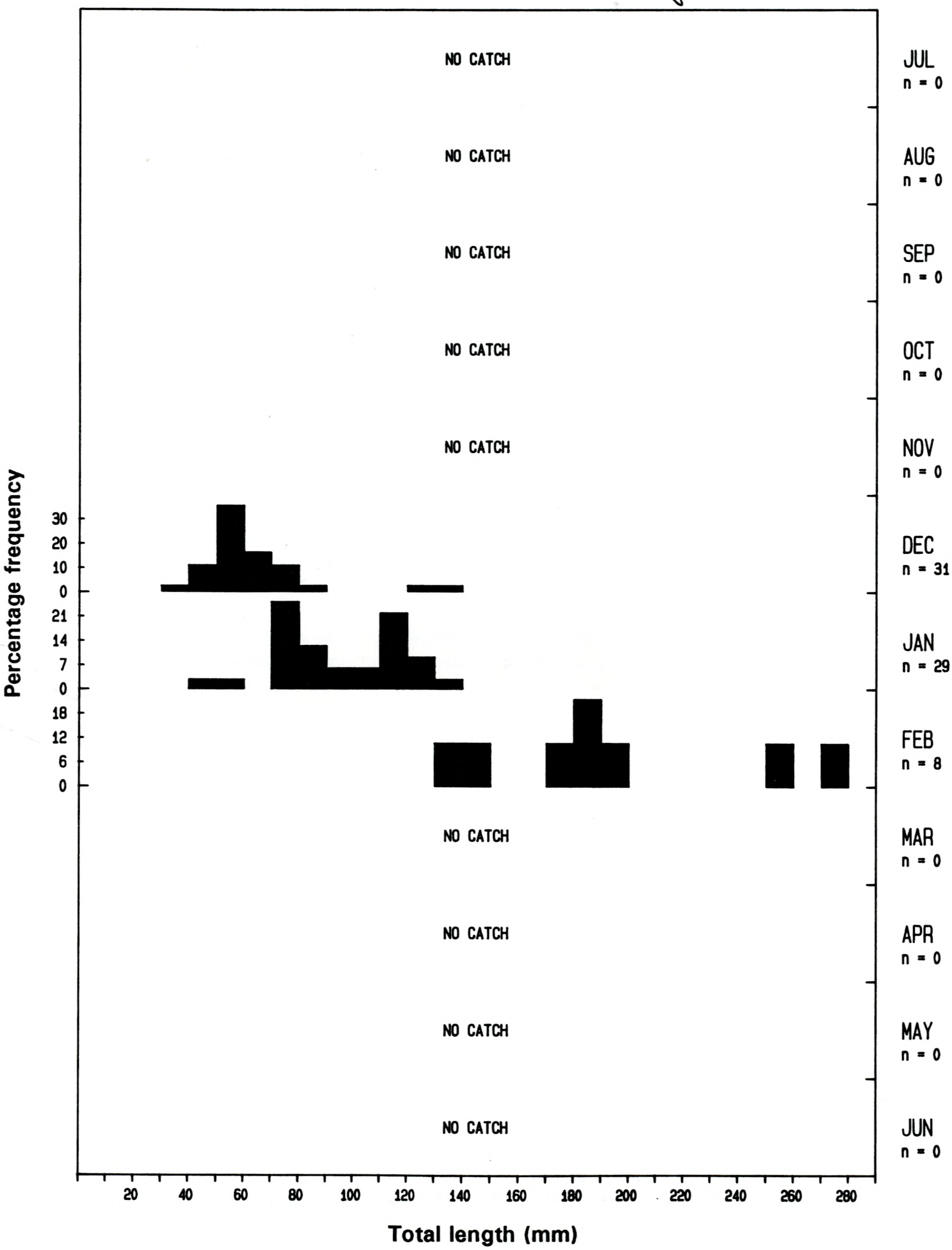
Knysna: *Lichia amia*



Bar Graph 21. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Lichia amia* in the Knysna estuary (n = number of fish in the sample).



Swartvlei: ***Lichia amia***



Bar Graph 22. Percentage length frequency distribution (1978-1980 data combined) of juvenile *Lichia amia* in the Swartvlei estuary (n = number of fish in the sample).

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ISBN 0-86810-232-6