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Resource partitioning by top predatory teleosts in the eastern Cape coastal waters (South Africa).

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ABSTRACT

A detailed feeding study of eleven inshore top predatory teleosts in the eastern Cape is presented. Material collected largely from line-caught fish was augmented by spearfishing. The predators were grouped according to habitat: pelagic, soft-sediment demersal and reef species. Pelagic fish examined were Lichia amia, Pomatomus saltatrix, Seriola lalandi, Atractoscion aequidens, Katsuwonus pelamis and Thunnus albacares. Stomach content analyses revealed that their prey varied according to size and between species. In coastal areas important prey species were Sardinops ocellata, Etrumeus teres, Engraulis capensis and Loligo reynaudi. The use of fish otoliths and squid beaks allowed accurate identification of the prey and their measurement provided details of their size composition. This has provided greater insight into the distribution of prey species and their importance in food webs.

The principal large predator of shallow coastal soft substrates is Argyrosomus hololepidotus, which takes pelagic and demersal prey. Important prey of small specimens are mysids, whereas fish and squid become more important in the diet of larger specimens (>300 mm). Fish prey include Sardinops ocellata, Engraulis capensis, Pomadasys olivaceum and A. hololepidotus. Loligo reynaudi is the dominant cephalopod prey. Selectivity of A. hololepidotus was investigated. Prey were compared to catches made during a small-mesh trawl survey. The absence of certain species from the diet suggests that they avoid predation, possibly by outswimming A. hololepidotus (e.g. P. saltatrix) while large Galeichthys feliceps are rare in the diet, probably because of their formidable spines. Flatfishes, P. olivaceum, juvenile G. feliceps and small A. hololepidotus appear to be preferred food items. The depth distribution of predators and prey is described, and it appears that the distribution of predators may be influenced by their prey.

Top predatory teleosts inhabiting coastal reefs are Cheimerius nufar, Petrus rupestris, Polysteganus praeorbitalis and Epinephelus guaza. Diet changes with size and locality but comprises small reef fishes for most of the sparids. C. nufar takes pelagic fish and squid more than the other predators while *P. rupestris* and *P. praeorbitalis* prey on cheilodactylids, clinids and other reef associated prey predominantly. *E. guaza* takes principally crabs and octopods.

Classification and ordination analyses of the prey taken illustrated the inter-relationships of predators, which change with increasing size. The pelagic predators are most similar to each other and *A. hololepidotus* is closer to this group than to reef predators. The reef predators are less similar to each other, although this group as a whole is segregated from pelagic predators. Exceptions to this are large *C. nufar* and large *P. praeorbitalis*, which fall into the pelagic predator group, as they took pelagic prey to a large extent. These results are discussed and the patterns shown are compared to other studies and current resource partitioning theory.

Two food webs are provided for the coastal waters of the eastern Cape. The pelagic food web has clupeids, engraulids and *L. reynaudi* as principal components. The reef system is more complex and the Clinidae, Cheilodactylidae and *Octopus* spp. are important. The use of food webs in management and in providing a framework for testing theoretical models is shown to be important. Research needs are identified and include more detailed work on the basic biology and ecology of the top predators and their prey.

CHAPTER 1

INTRODUCTION

Despite their importance in marine food webs, remarkably little work has been published on top predatory fishes in South Africa. Early work on predation in the western Cape was concentrated on commercially important trawl fish such as *Merluccius capensis* (Rattray 1947, Davies 1949), while more recently certain line fish have been examined by de Jager *et al*. (1963) and Nepgen (1970, 1977, 1982). In Natal the work of van der Elst (1976, 1979) and Bass *et al*. (1973, 1975a,b,c, 1976) has provided some information on prey of some top predators, namely elf (*Pomatomus saltatrix*) and sharks. Off the eastern Cape coast studies have been made of trawl fishes by Hecht (1976) and of the soldier, *Cheimerius nufar*, by Coetzee & Baird (1981a). Lasaik's (1982) study of surf zone fishes provided information on community composition and energy flow but limited data on piscivores. The results of these studies are reviewed where relevant in the thesis.

One of the major reasons for the limited work on the diet of top predatory fishes is that it is usually very difficult to identify well-digested prey. Fish bones and cephalopod 'beaks', which are more resistant to digestion, are often the only material remaining in the stomachs of top predators. Cephalopod beaks have been used widely outside South Africa to identify prey, following Clarke's (1962) description of beaks and publication of regressions to derive original prey weights. Although most of his work was concentrated on sperm whales and their prey (Clarke 1966, 1972, 1977, 1980), he and his colleagues have also used beaks to identify the prey of top predatory fishes (Clarke & Merrett 1972, Clarke & Stevens 1974). Similarly Pinkas *et al*. (1971) and Perrin *et al*. (1973) used these methods to identify stomach contents of tuna and porpoises. Although Wolff & Wormuth (1979) and Wolff (1982) have recently developed numerical methods to identify beaks, such methods were not adopted in this study as it has yet to be established that they hold in different geographical areas.

Fish otoliths have frequently been used for identification in predator-prey studies (Fitch & Brownell 1968, Pinkas *et al*. 1971, Perrin *et al*. 1973). Morrow (1979) noted the use of otoliths but recommended that direct comparisons should be made for reliable identifications, rather than illustrations.

Accurate identification of fish and cephalopods was possible in this study because the Port Elizabeth Museum has an extensive otolith and beak reference collection, which has been built up during the past ten years for prey identification in stranded marine mammals (Ross 1979).

The present field study was initiated to investigate the coastal predatory fishes and their prey in the eastern Cape between Mossel Bay (34°10'S, 22°08'E) and Kei River Mouth (32°41'S, 28°23'E). Because the aim of the programme was to study important top predatory teleosts, the ski-boat fishery was used as a field sampling method, as the anglers catch a variety of carnivorous fishes. Those studied in detail were two carangids, *Lichia amia* and *Seriola lalandi*; one pomatomid, *Pomatomus saltatrix* and two sciaenids, *Atractoscion aequidens* and *Argyrosomus holotepidotus*. Two scombrids, *Katsuwonus pelamis* and *Thunnus alabares*, were encountered seasonally. The sparid fishes studied in detail were *Petrus rupestris*, *Cheimerius nufar* and *Polysteganus praeorbitalis*. The only serranid studied was *Epinephelus guaza*.

Despite certain disadvantages, which will be detailed later, ski-boat sampling was most fruitful because this programme had limited logistical back-up. Diving observations were made whenever possible but these merely augmented sampling. Most of the data are derived from the identification and measurement of squid beaks and otoliths removed from predators' stomachs.

Preliminary observations revealed that the predators are usually found either pelagically over soft, sandy substrates or over reefs. In the following chapters the predators and their prey are grouped according to their habitat preference, and their ontogenetic, seasonal and areal changes of diet are described. At the end of each chapter general findings are discussed and compared to other studies. A similarity analysis is presented in Chapter 7 to synthesize information on the predators. Food webs for inshore eastern Cape teleost top predators are presented in Chapter 8 and the findings are discussed in the light of other resource partitioning studies.

CHAPTER 2

PHYSICAL FEATURES OF THE EASTERN CAPE

Currents

The Agulhas current is a dominant feature of the south west Indian Ocean circulation. Formed south-west of Madagascar by the uniting of the Mozambique and East Madagascar current, it flows close inshore along the south-east African continental shelf. An extremely powerful current, it has been estimated that the mass transport over 2500 m is about 80 Mtons/s in summer and 100 Mtons/s in winter (Heydorn *et al*. 1978).

The eastern boundary is formed in a region of weak gradients where current speed and temperature decline irregularly with distance from the coast. The current is fast flowing. The core velocity exceeds 1m/s and can attain 2.5m/s, but shows no pronounced seasonal change. The surface temperature here varies from about 27°C in March (autumn) to 22°C in August (winter). The western, inshore boundary is marked by a strong surface temperature gradient of 1 to 2°C in 10 km, although there is rarely an accompanying salinity change. Central water lies beneath the current in depths of 200 to 800 m and its temperature and salinity decrease with depth (Heydorn *et al*. 1978).

The Agulhas current lies close inshore off Natal, normally meandering over a short range (Fig. 1). However, meanders up to 100 km wide have been recorded (Heydorn *et al*. 1978, Lutjeharms 1981) and cyclonic eddies are often found inshore of the current boundary. South-east of Cape Morgan the current moves away from the coast, following shelf contours (Fig. 1). As the continental shelf broadens the current moves off to about 350 or 400 km offshore and becomes an 'unstable jet' (Harris 1978). Disturbances in the current upstream of Port Elizabeth remain small probably because of its proximity to the coast. These meanders subsequently grow along the Agulhas Bank where warm water plumes and shear-edge eddies are formed and mirrored on the southern edge of the current. With the dispersion and disintegration of shear-edge features, warm filaments infiltrate onto the Agulhas Bank and into the

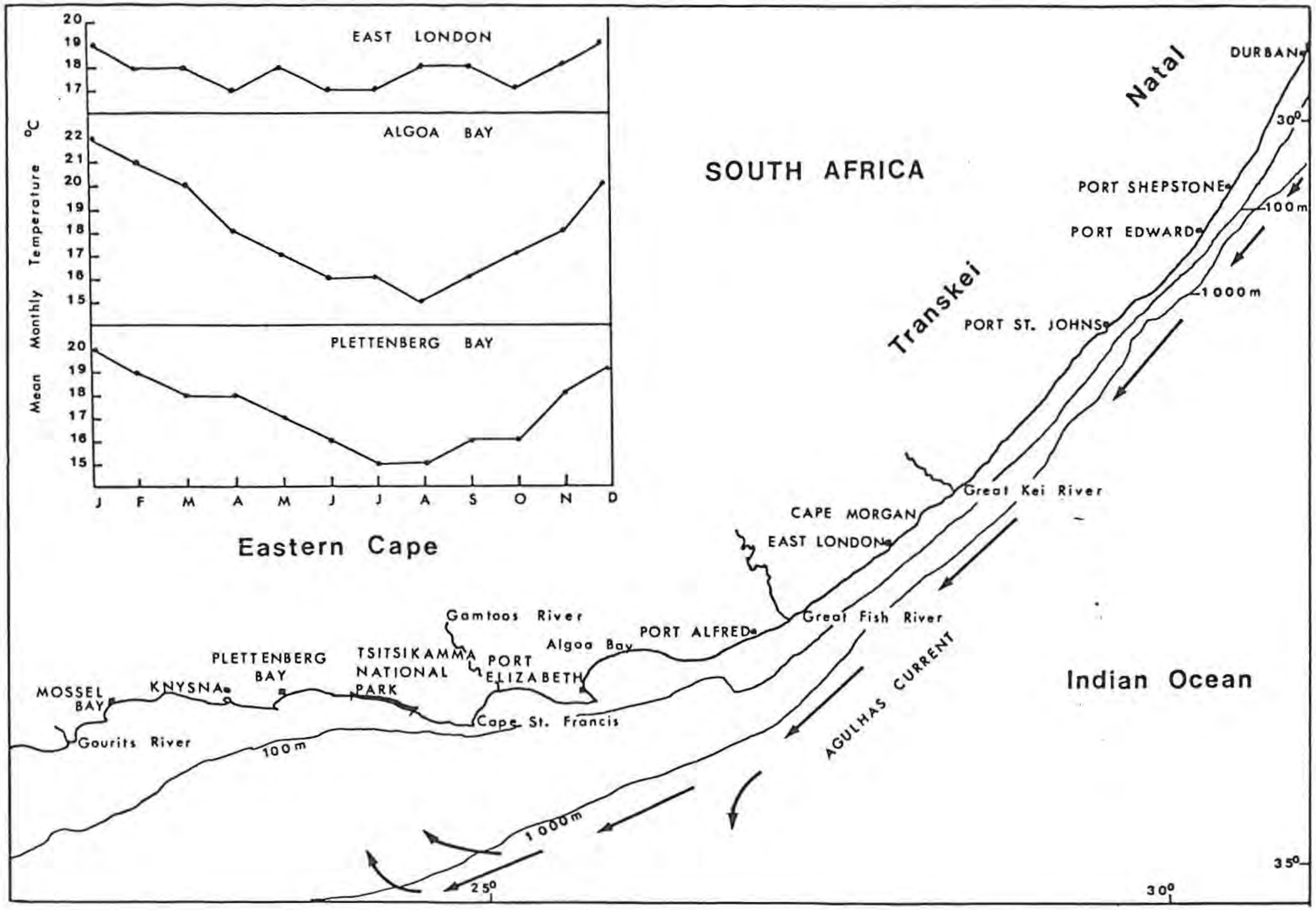


Fig. 1. The south east coast of South Africa showing Natal, Transkei and the eastern Cape. The Agulhas Current is shown diagramatically. Inset , the mean monthly surf temperatures of East London, Algoa Bay and Plettenberg Bay.

South Atlantic Ocean. Large Agulhas current rings may also be formed and advected into the South Atlantic Ocean while the bulk of the current eventually turns south, then eastwards (Lutjeharms 1981).

The movement of shelf water is influenced both by the Agulhas current and by wind movement (Harris 1978). The predominant wind direction is parallel to the coast and changes direction according to high pressure systems or low pressure frontal systems which tend to move along the coast in a south-westerly direction. The region is subject to strong winds in all seasons of the year. The limited data for this region suggest that both counter currents, which are probably variable and short lived in duration, and north-east flowing currents influence coastal waters. However, evidence from ship drifts is apparently contradictory indicating net eastward flow (Harris 1978). Drift-card studies currently underway (Baird pers.comm.) may help to resolve these discrepancies. In Algoa Bay water movement is caused predominantly by cyclonic currents. Wave-induced currents affect the nearshore zone and are responsible for littoral sand movements by cellular and longshore systems.

Upwelling is a feature of the southern Cape coast and is associated with winds with an easterly component. The climatic conditions responsible occur most frequently in spring and summer, although upwelling has been recorded in all seasons. East-pointing capes appear to be important in its triggering (Schumann et al. 1982). Associated with upwelling are drastic temperature changes of 5 - 10°C, which have been known to stun fish (Winch 1982 and pers. obs.) and must have a major influence on the biota of this region. Mean monthly surf temperatures from East London, Algoa Bay and Plettenberg Bay are shown in Fig.1.

The coastal water is often separated by a thermocline of about 11°C between 15 and 35 m in summer (Schumann et al. 1982 and pers. obs.). Warm green or clear water overlies a cooler turbid layer in which visibility may be reduced to zero. The cause and origin has not been described but the turbidity is probably derived from fine sediments of riverine origin. Over reef systems visibility is sometimes better.

The major rivers feeding Algoa Bay are the Swartkops and Sundays which transport both organic matter and alluvial sediments into the bay.

Extensive fine sand and silt beds in this part of the bay increase the turbidity of the water considerably over most of the year (per. obs.; Fig. 2).

A characteristic feature of this region is the enormous half-heart bays protected by east-jutting headlands. Long stretches of sandy beaches with extensive dune systems predominate. Sand flats also occur underwater between reefs. In Algoa Bay massive reefs are associated with St Croix, Brenton and Jaheel islands and the Bird Island complex as well as Riy Bank. Further north the coast is similar, particularly at East London which provides a rich fishing ground.

The south Cape coast has rugged, folded cliffs. The quartzites in the Table Mountain Sandstone system resist erosion and form underwater reefs which are similarly folded, providing caves and cracks in which animals can hide. These features are pronounced between Knysna and Cape St Francis, particularly in the Tsitsikamma Coastal National Park.

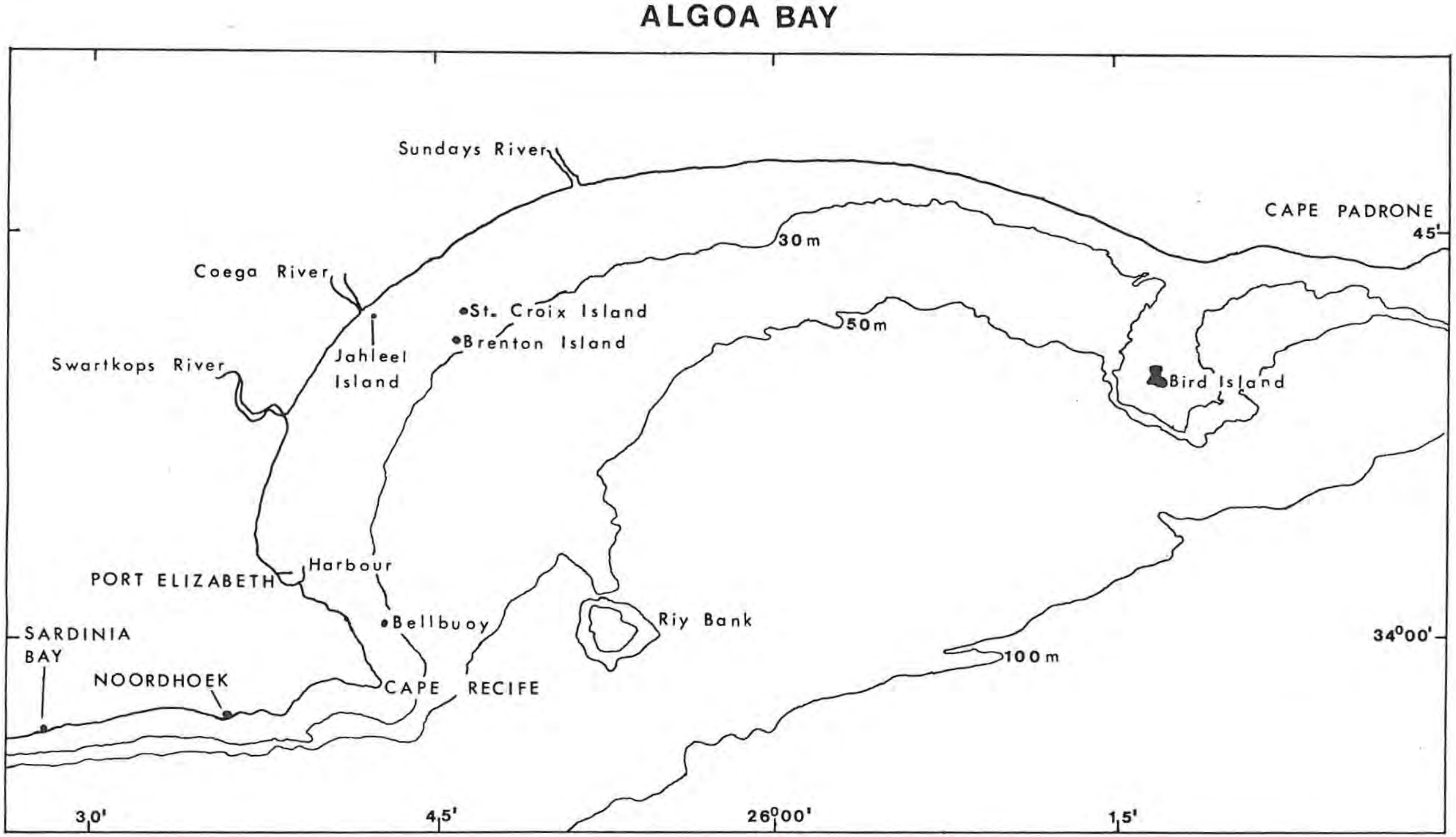


Fig. 2. Algoa Bay and environs showing places mentioned in the text.

CHAPTER 3

MATERIALS AND METHODS

Sampling

This study was initiated in February 1978 and continued to May 1982, and was run concurrently with an investigation of the biology of the fishes caught by ski-boat anglers in the eastern Cape. The study was undertaken in three phases. From the beginning of 1978 to the end of 1980 the major ski-boat launching sites were visited every weekend that weather permitted fishing. For logistical reasons most material was collected from the Port Elizabeth Deep Sea Angling Club. Other clubs from which material was obtained were the Noordhoek and Sardinia Bay Clubs. Kei River mouth and Mossel Bay were the respective north eastern and western limits of sampling. These areas were visited occasionally during 1979 and 1980. Changeable and inclement weather and the few boats operating from these areas mitigated against more frequent sampling. After 1980 line-caught fish were sampled occasionally until 1982.

From January 1980 to May 1982 a diving programme was run in Algoa Bay and the Tsitsikamma Coastal National Park in order to observe fish in the wild and to augment angling material with speargun-collected fish.

During 1980 the RMV Thomas B. Davie was commissioned by the Port Elizabeth Museum to undertake a trawling survey of nearshore areas to determine the occurrence of marine nursery areas of estuarine-associated fish (Wallace et al. in prep.). Large numbers of small piscivorous fish were caught in these trawls and information on their depth distribution and feeding has been prepared by Smale (in prep.). In addition, large Argyrosomus hololepidotus caught in those trawls were included in this study. Finally, fish were obtained from experimental gill nets or beach seines used by the Port Elizabeth Oceanarium.

The ski-boat fishery is made up of both amateur and commercial fishermen and the boats travel from one to about 40 km from the launching site. Although inshore (<8 km from shore) angling is most common, a few boats fish at the edge of the continental shelf or in eddies of the Agulhas Current (8 to 40 km offshore) where pelagic gamefish are often encountered. More than twenty species of fish are frequently caught and a variety of fishing methods are used. These include trolling fish-like lures and metal spoons and the use of cut and whole baitfish and squid. Fish caught from a wide variety of areas and depths were sampled in this way. Hence both pelagic and demersal species were available for sampling. Although the distances used for inshore and offshore angling are arbitrary, they are distances normally adhered to by anglers.

As many ski-boat catches as possible were examined each day and the entire catch was of each was sorted, identified and measured, and a subsample was weighed. Each fish was gutted and the stomachs which had not been everted were placed in labelled bags and kept on ice until processed in the laboratory, usually later that day. The fishing locality, depth, bait used and other observations made by the crew were recorded with the biological information. Data was collected in a similar way from spearfishing competitions and from experimental catches.

Diving observations were made using standard SCUBA and snorkel equipment in Algoa Bay and Tsitsikamma Park. Spearguns, Hawaiian slings and rotenone were used to sample small reef fish which were unavailable from ski-boat catches, and to compare stomachs collected using different methods. Underwater observations were noted on a perspex slate. Diving expeditions were limited because of logistical problems with back-up requirements and because turbid and rough water was encountered very frequently.

Observations were also made on piscivorous fishes held in the main fish tanks of the Port Elizabeth Oceanarium. This circular tank has a diameter of 20 m, is about 2.5 m deep and includes artificial reefs. A variety of locally caught fishes is maintained for display and notes were made of the interactions of two predators, Lichia amia and Cheimerius nufar, and small prey fishes.

Laboratory procedures

In the laboratory, stomachs were opened and the contents sorted, counted and weighed on a top pan balance to the nearest 0.1 g once excess moisture had been drained off. Bait was easily recognised and discarded. Otoliths were either removed from fish skulls or collected loose. Buccal masses were removed from cephalopods and the beaks collected. Other invertebrates were preserved in 10% formalin for later counting and identification. The entire stomach contents and stomach wall were carefully washed in a red plastic bowl which allowed both squid beaks and fish otoliths to be seen easily. A centrifugal flow of water was used which caused loose otoliths to settle in the centre. Free cephalopod beaks were removed from the bowl or from a sieve through which the remains were passed after washing. Otoliths were stored dry in labelled vials and cephalopod beaks were preserved in 10% formalin.

Neither formalin nor alcohol was used in field storage of stomach contents as otoliths are etched or made brittle, providing inaccurate measurements or material which is too etched for accurate identification.

Otoliths were examined under a binocular microscope and compared to material held in the extensive collection of the Port Elizabeth Museum. Owing to the complexity of otolith morphology and variations within families, direct comparison with identified material was found to be the best method of identification. Otoliths of oceanic forms were difficult to identify and Mr J. Fitch (Department of Fish and Game, California) kindly assisted with initial identifications. These "types" were then used as a comparison with collected material. The identity of even slightly digested prey was confirmed using otoliths. Otoliths were paired when possible and the highest number of either left or right otoliths counted. Measurements of undigested otoliths were to the nearest 0.01 mm. Digested otoliths were obvious because of their chalky eroded appearance and these were not measured.

Cephalopod beaks were paired and the highest number of either upper or lower beaks was counted. These were identified by comparison with reference material held in the museum collection and by reference to the literature (Clarke 1962; Pinkas _et al_. 1971). Furthermore, examination of material at the Cephalopod Beak Identification Workshop at Plymouth, England in June 1981 (Clarke _in prep._), further aided identification.

Beaks were measured according to Clarke (1962) using measuring calipers for those larger than 2 mm and a binocular microscope for smaller specimens.

Crustaceans were counted and weighed. In most cases no problems were encountered as individual crabs etc. could be recognised and counted using carapaces or chelae. Mysids and euphausids were counted using the number of eye pairs and when very large samples were encountered a subsample was weighed, counted, then the total number in the total sample calculated. A list of prey is given in Appendix Table 1.

Analysis of data

The data was coded and captured onto the Port Elizabeth Museum's Hewlett-Packard 9835 computer. Programs for data capture and analysis were written by Dr H.M. Kok, Port Elizabeth Museum. Similarity analyses and multidimensional scaling programmes were run on the University of Cape Town's UNIVAC 1100 computer (Chapter 7).

1. Relationships of prey length to predator fork or total length (see below) were plotted on scatter diagrams. The predator length was measured and the fish prey total or cephalopod mantle length were calculated using the regression values presented in Appendix Table II.
2. Analysis of stomach contents was by frequency of occurrence where the number of times that a prey organism is represented in a stomach is summed and presented as a percentage.

   The numerical method: The number of a particular prey item is given as a percentage of the total number of prey items taken.

   The gravimetric method: The mass of a prey item is divided by the total mass of prey and presented as a percentage. Throughout this thesis original wet mass is used, despite shortcomings of differential digestion rates of prey (Hyslop 1980). As this was primarily a field study it was beyond the scope of this programme to overcome this problem with experimental digestion studies for each predator. Although reconstituted stomach content weights could have been calculated, digestion rates were further complicated by large otoliths (e.g. Sciaenidae and Sparidae) resisting erosion while small otoliths are digested rapidly once exposed. Cephalopod beaks are also retained in stomachs and this compounds errors using reconstituted masses. Because of these problems, original wet masses were used. The use of percentage frequency %F, percentage number %N and percentage mass %M overcomes the disadvantage of using only one of these methods (Hynes 1950, Windell 1971, Hyslop 1980). For each predator a table is given of values (to the nearest 0.1%) and index of relative importance (IRI) diagrams showing %F, %N and %M are given for the principal prey (Pinkas et al. 1971). Principal prey were regarded as those which contributed more than 4% to the diet in more than one method of analysis. Combinations of these values in IRI indices were not used as they may compound sources of error (Hyslop 1980). Regurgitation of stomach contents and the probable differential digestion rates of prey suggest that values obtained in this study are not highly accurate. Figures are given to one decimal place in the tables to facilitate recalculations of original weights and numbers but are rounded to the nearest whole number in the text.

3. Predator length groupings were decided by a preliminary examination of the stomach data and were used to gain insight into prey changes with increase in predator size. The number of groups used depended on the sample size and length range of material.

4. Indices of fullness were calculated for each predator to determine maximum stomach fullness. The formula used in calculation was after Windell (1971):

$$\text{fullness index} = \frac{\text{mass of stomach contents}}{\text{mass of predator}} \times 100$$

5. Reconstituted stomach mass was calculated for individual items in predators' stomachs using the otolith or beak measurements from which the mass of each item in a predator's stomach was then summed. Regression values are shown in Appendix Table 2. Original wet masses had to be used for those prey not listed, such as crustaceans, where no regression values were available. The index was calculated after Windell (1971):

$$\text{consumption index} = \frac{\text{reconstituted mass of stomach contents}}{\text{mass of predator}} \times 100$$

The high frequency of regurgitation and partial regurgitation found in this study prevented meaningful comparisons of mean fullness or mean consumption indices. Overall means were, however, calculated for the tunas for comparison with other studies. The lower numbers recorded for consumption indices result from well digested otoliths being the only remains in stomachs and these were not used in calculations.

6. Index of food similarity was calculated for each size group of predator. The method used is described in detail in Chapter 7.
7. Prey selectivity was calculated for A. hololepidotus, the only species for which adequate data on the occurrence of prey in the environment had been collected. This is described in detail in Chapter 5.
8. The Shanon-Wiener diversity index was used to compare the diets of predators to reveal the specificity of prey selection (Chapter 8). The Shanon-Wiener function is expressed as;

$$H = -\sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

where H = information content of sample
= index of species diversity
S = number of species
pi = proportion of total sample belonging to ith species.

The use of log 2 provides data on "bits per individual". The information content is a measure of uncertainty so that the larger the value of H, the greater the uncertainty. This may be directly related to the diversity of a sample (Odum 1971, Krebs 1978). This measure is widely used in ecological studies (e.g. Ogden & Ebersole 1981, Lasiak 1982), and was adopted to compare diets of fishes with each other and with Lasiak's study of a fish community in Algoa Bay. Lasiak (1982) provides a summary of other marine and estuarine studies in which this measure has been used.

Measurements

The body length measurements of all the predators with forked tails is the fork length (FL) from the tip of the snout to the end of the caudal ray in the middle of the tail. These species are: Lichia amia, Pomatomus saltatrix, Seriola lalandi, Petrus rupestris, Atractoscion aequidens, Polysteganus praeorbitalis, Katsuwonus pelamis and Thunnus albacares. Total lengths (TL) of Argyrosomus hololepidotus and Epinephelus guaza were used as they have truncate and convexly rounded tails respectively. Their length was measured from the tip of the snout to the end of the longest caudal ray bent to the midline.

Body lengths of teleost prey are all described as total lengths (TL) for consistency, although the entire range of tail shapes was encountered with the prey. Dorsal mantle lengths (DML) were used for cephalopods, except that ventral mantle lengths (VML) were used for Loligo reynaudi. Carapace widths were measured for crabs. Carapace length was used for all other crustaceans except mysids, for which total length was used.

Identification critique

The use of cephalopod beaks and fish otoliths facilitated identification and the majority of prey were identified to species. However, there were some taxonomic and identification problems which are briefly mentioned here.

Crustacea were identified using the available literature but, as many of the keys depend on surface details and appendages, both of which are often digested, it was often impossible to identify beyond the family level. Had it been feasible to use a chemical preservative in the field, identifications of this group may have been more accurate.

Some difficulties were encountered with oceanic cephalopods, especially juveniles. As a result it was not possible to identify these prey beyond family level (e.g. Ommastrephidae). Pelagic octopods also proved difficult to identify unless they were undigested. These problems are commonly encountered (Clarke in prep.).

Teleosts were identified with a high degree of confidence except when juveniles or small Clinidae or Gobiidae were encountered. Juvenile fishes often have undifferentiated otoliths while the Clinidae and the Gobiidae are difficult to identify and are poorly represented in the Port Elizabeth Museum reference collection.

CHAPTER 4

PELAGIC PREDATORS

In this chapter the prey of six pelagic predators are described and discussed for each species. The findings are discussed in relation to current knowledge of prey biology and behaviour.

Family: Carangidae Lichia amia (Linnaeus, 1758)
Common name: leervis

Description

Adult Lichia amia have elongate, laterally compressed bodies (Fig. 3 fold-out under back cover). Body depth is 29 - 39% FL. With the dorsal and anal fins erect, this depth increases to about 57%. The dorsal and anal fins are without finlets, the caudal is deeply forked and the caudal peduncle relatively stout. The maxilla extends beyond the orbit. The gape is about 9% FL. Relatively small teeth occur on the dentary, premaxilla, palatines and vomer. Dentary and premaxillary teeth are slender, pointed and arranged in a broad band. Adults are grey-green dorsally and laterally, and white ventrally.

Distribution

Lichia amia is found in the Mediterranean, eastern Atlantic and the south-west Indian Ocean along the coast of southern Africa to Delagoa Bay, Mozambique (Smith 1972, Smith-Vaniz & Staiger 1973).

Habitat

L. amia is an inshore species usually seen patrolling the sublittoral zone, often at the break-point of advancing waves near sandy beaches, shallow reefs and headlands. Although they often occur over shallow reefs and sand at about 10 m, they have been caught by ski-boat anglers down to depths of 20 m in Algoa Bay during this study. Smith-Vaniz & Berry (1981) found L. amia to a depth of at least 50 m. Both juvenile and adult L. amia enter estuaries (Wallace 1975, Wallace & van der Elst 1975, Winter 1980, Marais & Baird 1980a & b, Coetzee 1982, Beckley pers.comm., Smale & Kok in prep.).

L. amia occur in the southern and eastern Cape all year round although adults migrate to Natal in winter and spawn in spring (van der Elst 1981). They return to the Cape in late spring and summer. Maturity is attained at about 600 mm FL (van der Elst 1981). Larvae are apparently transported by the Agulhas current from Natal to the Cape, and juveniles are found in estuaries and the sea (Smale & Kok in prep., Lasiak 1981, Coetzee 1982). In Algoa Bay leervis are most commonly encountered near the harbour breakwater, Swartkops River Mouth, St Croix and adjacent islands and the Bellbuoy (Fig. 2).

Material

A total of 269 L. amia specimens of 314 - 1200 mm FL were sampled. Seventy five (28%) had food remains in their stomachs. Although partial and total regurgitation was observed, it was not possible to quantify. Those with prey remains measured 455 - 1200 mm FL (Fig. 4). The fullest stomach recorded in this study was 5.4% of the predator mass. The highest reconstituted stomach mass was 8.9% of predator mass.

Prey

The prey of L. amia is shown in Table 1, where the data are separated according to size. The principal prey are shown in Fig. 5.

Small L. amia (401-700 mm) predominantly take schoolng pelagic teleosts (76% by number, 79% by mass). The most important were Trachurus trachurus, Engraulis capensis and Scomber japonicus, which accounted for 70% of the diet by mass. This predator group had an average of 4.2 items in each stomach, indicating that several small fish are taken during a feeding period. Post-larvae and juveniles were frequently recovered, but were difficult to identify, as neither the entire specimens nor their otoliths were differentiated. These are shown as "unidentified fish" in Table 1. Demersal schooling prey, A. hololepidotus, U. canariensis, P. olivaceum, P. natalensis and C. nufar, were taken less (15% by number and 19% by mass). Pagellus natalensis was the most important prey of this group by all methods of analysis. The only invertebrate was Macropatasma africanum, a common schooling penaeid prawn which is found over sandy areas and reefs.

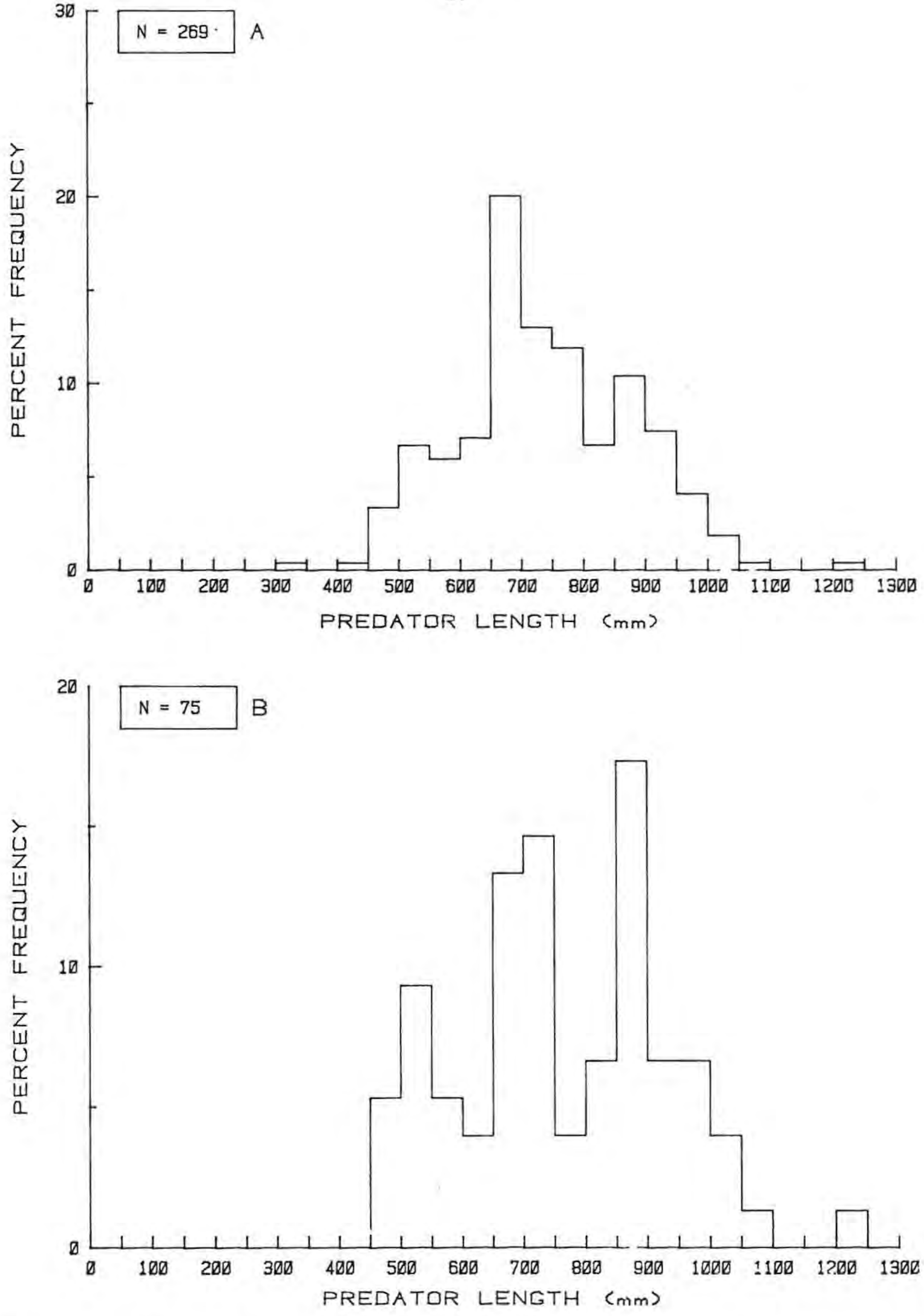


Fig. 4. Histograms of the total sample of Lichia amia (A) and those with stomach contents (B).

Table 1. The prey of *Lichia amia* according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M),g.

Prey	401 - 700 mm FL			701 - 1200 mm FL			401 - 1200 mm FL		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA									
Macropatasama africanum	3.6	3.3	0.1				1.3	1.8	<0.1
MOLLUSCA									
Sepiidae				2.1	1.0	4.7	1.3	0.5	3.6
OSTEICHTHYES									
Unidentified fish	21.4	5.0	1.4	6.4	3.0	0.2	12.0	4.1	0.5
Etrumeus teres	7.1	2.5	5.7	8.5	5.1	2.0	8.0	3.6	2.9
Sardinops ocellata	7.1	2.5	4.3	36.2	35.4	39.2	25.3	17.3	31.0
Engraulidae				4.3	2.0	0.1	2.7	0.9	<0.1
Engraulis capensis	39.3	51.2	24.3	25.5	18.2	5.2	30.7	36.4	9.8
Trachurus trachurus	17.9	14.9	32.3	4.3	7.1	3.9	9.3	11.4	10.6
Pomatomus saltatrix				2.1	2.0	0.8	1.3	0.9	0.6
Argyrosomus hololepidotus	3.6	1.7	0.1	2.1	1.0	3.2	2.7	1.4	2.5
Umbrina canariensis	3.6	0.8	0.1				1.3	0.5	<0.1
Pomadasys olivaceum	10.7	3.3	0.7				4.0	1.8	0.2
Sparidae	3.6	0.8	0.1				1.3	0.5	<0.1
Cheimerius nufar	10.7	3.3	7.4				4.0	1.8	1.8
Pagellus natalensis	14.3	5.8	10.6	17.0	14.1	17.0	16.0	9.5	15.5
Scomber japonicus	10.7	3.3	11.4	10.6	8.1	17.0	10.7	5.5	15.7
Liza richardsoni	3.6	0.8	1.0	4.3	2.0	2.6	4.0	1.4	2.2
Myxus capensis				2.1	1.0	4.1	1.3	0.5	3.1
Sphyraenidae	3.6	0.8	0.3				1.3	0.5	0.1
Totals	28	121	762.8	47	99	2463.9	75	220	3226.7

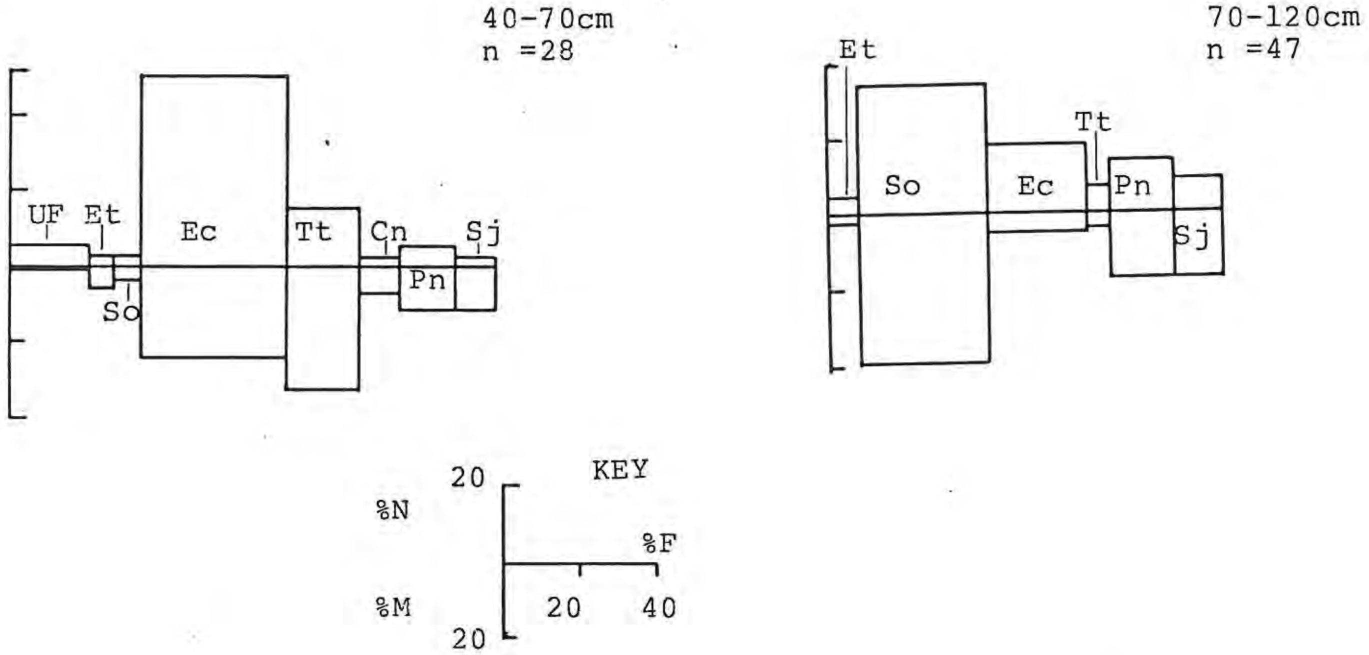


Fig. 5. The principal prey of Lichia amia.

Cn:Cheimerius nufar Ec:Engraulis capensis Et:Etrumeus teres Pn:Pagellus natalensis
Sj:Scomber japonicus So:Sardinops ocellata Tt:Trachurus trachurus UF:Unidentified fish

Large L. amia (701-1200 mm) took predominantly schooling pelagic prey (81% by number and 75% by mass). Sardinops ocellata and Scomber japonicus were dominant. Engraulis capensis was important by frequency and number but, owing to its small size, it was not important by mass. Demersal schooling fish were taken to a lesser extent (15% by number, 20% by mass). Pagellus natalensis was the most important prey of this group. Argyrosomus hololepidotus was less dominant. One specimen of Sepiidae was taken but no other cephalopods and no Penaeidae were recorded from large leervis. An average of 2.1 prey items per stomach was recorded. The two groups were 39% similar according to prey mass.

Predator-prey size relationship

A scatter diagram of the length of prey plotted against predator length is shown in Fig.6. With increasing predator length there is an increase in the maximum size of prey taken, although a wide range is found. The highest ratio was 47% and the lowest 1.3% of the predator length. The narrow range of prey size found with large predators may partly be a reflection of the fewer data available. Most prey are between 10 - 30% of predator length. One cause of the data spread in the scatter diagram is that predators over a wide size range prey opportunistically on highly abundant small schooling prey. This was evident during sampling and to illustrate this trend five of the more important prey of small (401 - 700 mm) and large (701 - 1200 mm) leervis are shown in Fig.7. A wide range of prey sizes are taken but the tendency is for larger leervis to take larger prey. This is most marked in prey species such as S. japonicus and P. natalensis. There is, however, often an overlap in the range taken, especially of smaller pelagic schooling fishes.

Seasonality

Seasonal variations in prey taken by L. amia were investigated by grouping stomach contents according to bi-monthly periods. Low numbers prevented subdivision according to size. Most stomachs (59), were collected between March and June, but the low numbers through the rest of the year make generalisations dubious.

Table 2 shows that S. ocellata is taken throughout the year. E. capensis was recorded from November to June and P. natalensis from November to April. Other prey species were taken intermittently with the highest

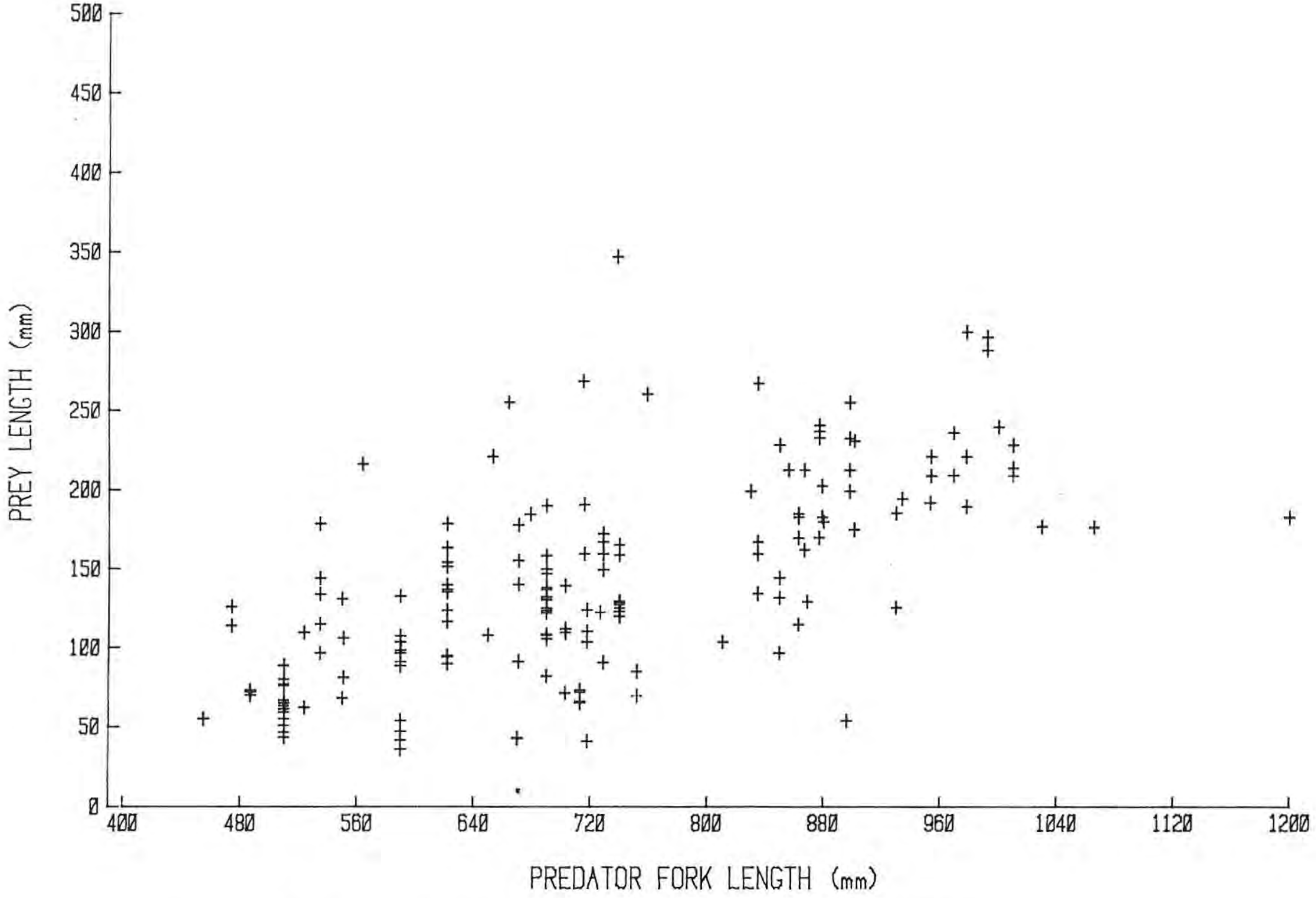


Fig. 6. Scatter diagram of prey length against fork length of Lichia amia. The dot represents a crustacean, fishes are shown by crosses.

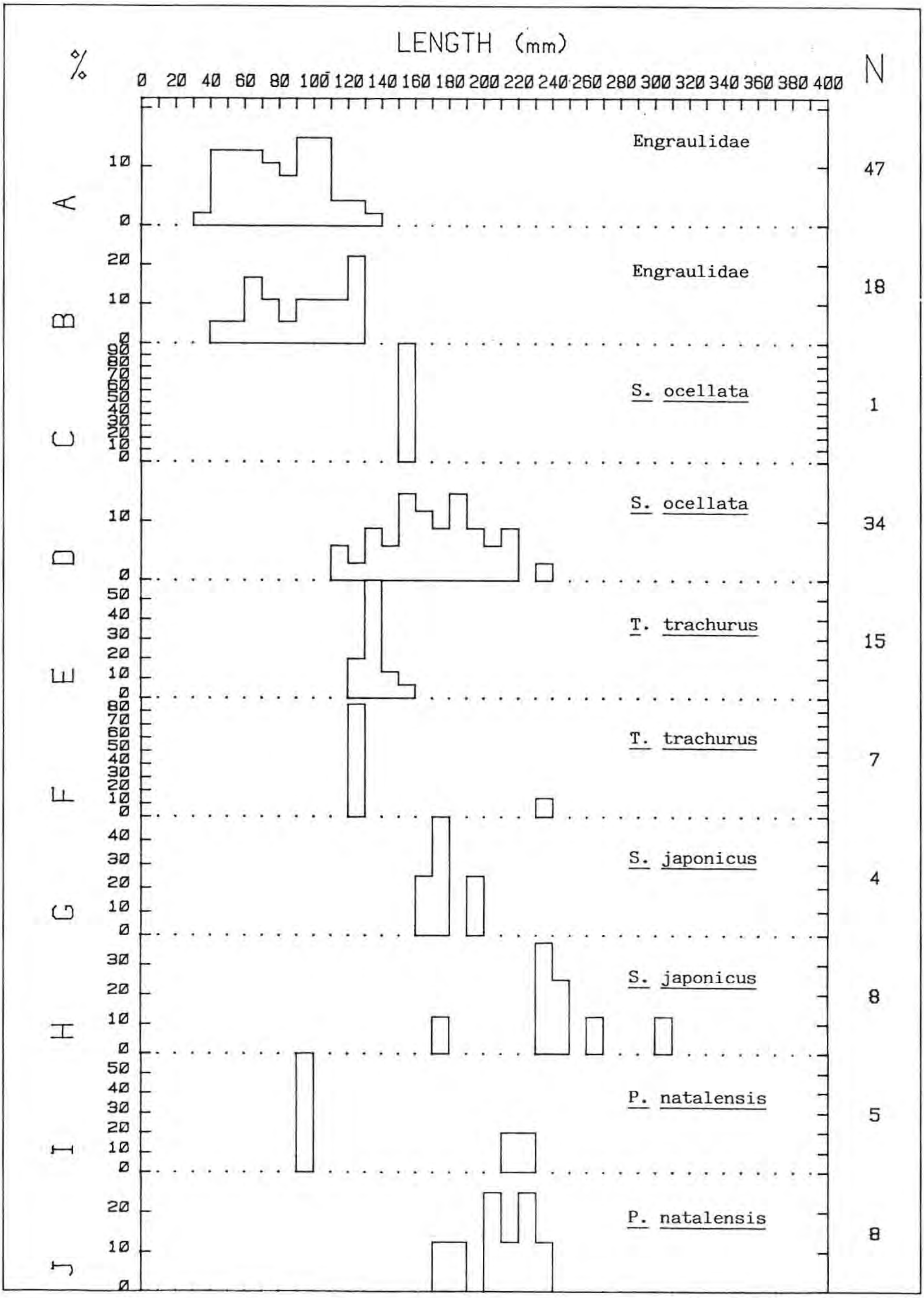


Fig. 7. Histograms of common prey of two size groups of *Lichia amia*. Fig. 7A,C,E,G and I were taken from *L. amia* <700 mm; B,D,F,H,J from *L. amia* >700 mm. They are: Engraulids (A,B); *S. ocellata* (C,D), *T. trachurus* (E,F); *S. japonicus* (G,H) and *P. natalensis* (I,J).

Table 2. The prey of *Lichia amia* taken in bimonthly periods, all years, combined. The totals are number of stomachs (F), number of items(N), and prey wet mass (M),g.

	January-February			March-April			May-June			July-August			September-October			November-December		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA																		
Macropatasma africanum				2.3	3.5	<0.1												
MOLLUSCA																		
Sepiidae				2.3	0.9	5.5												
OSTEICHTHYES																		
Unidentified fish				16.3	6.1	0.7	12.5	4.5	0.4									
Etrumeus teres				11.6	5.2	4.0										25.0	18.2	29.4
Sardinops ocellata	37.5	14	75.7	20.9	15.7	17.5	18.8	13.6	36.1	50.0	33.3	23.5	100	100	100	25.0	27.3	50.0
Engraulidae				2.3	0.9	<0.1	6.3	2.3	0.1									
Engraulis capensis	25.0	74.4	8.8	20.9	15.7	4.7	68.8	65.9	48.7							25.0	9.1	5.9
Trachurus trachurus				14.0	20.9	16.2										25.0	9.1	0.9
Pomatomus saltatrix							6.3	4.5	5.8									
Argyrosomus hololepidotus				2.3	0.9	3.8										25.0	18.2	2.9
Umbrina canariensis																25.0	9.1	2.1
Pomadasys olivaceum				7.0	3.5	0.3												
Sparidae							6.3	2.3	0.3									
Cheimerius nufar	12.5	2.3	1.3	2.3	0.9	1.0	6.3	4.5	8.2									
Pagellus natalensis	25.0	7.0	7.5	20.9	14.8	21.8										25.0	9.1	8.8
Scomber japonicus	12.5	2.3	6.7	14.0	8.7	18.7				50.0	33.3	47.1						
Liza richardsoni				4.7	1.7	1.0				50.0	33.3	29.4						
Myxus capensis				2.3	0.9	4.8												
Sphyraenidae							6.3	2.3	0.6									
Totals	8	43	507.2	43	115	2104.8	16	44	346.7	2	3	170	2	4	64	4	11	34

number in March-April when most stomachs (43) were collected. The low sample number over much of the year limits interpretations of prey preference.

Annual variation

Analyses of prey taken by *L.amia* on an annual basis suggested that there was some change with time (Table 3). The principal species, *S. ocellata* and *E. capensis*, switch in dominance after 1979. *E. capensis* became more dominant in 1980 and 1981, although *S. ocellata* was still important by mass in 1980. *P. natalensis* remained an important prey in each year. Other fluctuations are relatively small and may be accounted for as sampling variation.

Hunting behaviour

Three kinds of hunting behaviour were seen in *L. amia*. These depended on prey type. The first two were seen in the Port Elizabeth Oceanarium main tank, the third in the field, and a fourth is postulated.

1. The hunter slowly swims up to a school of mullet on the surface, usually from below and behind. When about four body lengths away, it accelerates and dashes at one of the school members. Hobson (1966) noted that a predator has a distinct advantage when prey are illuminated against the relatively bright water surface while the predator is in relative darkness, especially at twilight. Furthermore, by attacking from below and behind they are in the preys' "blind spot". Both lone predators and a pair of predators were observed attacking. No co-operation was evident, as the second fish merely followed the first, thus conforming with Major's (1978) observations on another carangid, *Caranx ignobilis.*
2. The second hunting tactic was seen when pursuing demersal prey such as *Pomadasys olivaceum* and *Lithognathus mormyrus* near reefs in the aquarium. The predators slowly approached the loose school of prey, accelerating to chase an individual which apparently escaped behind a rock or reef. Although *L. amia* turns quickly, the smaller prey seemed to be at an advantage as they twist away more rapidly. Similar observations have been made in the wild by Potts (1981) studying the interactions of *Caranx melampygus* with reef fishes off Aldabra.

Table 3. The prey of *Lichia amia* taken in different years of the study. The totals are numbers of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	1978			1979			1980			1981/82		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Macropotasma africanum										20	9.5	1.1
MOLLUSCA												
Sepiidae	4.5	2.9	14.9									
OSTEICHTHYES												
Unidentified fish	22.7	14.3	1.5	18.8	9.7	0.2	3.1	0.9	0.2			
Etrumeus teres	4.5	2.9	1.9	12.5	9.7	4.6	9.4	3.6	2.9			
Sardinops ocellata	36.4	34.3	26.6	25.0	41.9	46.5	21.9	11.6	29.7			
Engraulidae				6.3	3.2	0.2	3.1	0.9	<0.1			
Engraulis capensis	9.1	5.7	2.3	12.5	6.5	3.2	50.0	37.5	12.8	60	81	50.1
Trachurus trachurus	9.1	5.7	1.8				15.6	20.5	17.9			
Pomatomus saltatrix	4.5	5.7	2.6									
Argyrosomus holelpidotus							6.3	2.7	4.4			
Umbrina canariensis							3.1	0.9	0.1			
Pomadasys olivaceum	4.5	2.9	0.3	12.5	9.7	0.6						
Sporidae							3.1	0.9	0.1			
Cheimerius nufar							6.3	2.7	2.7	20	2.4	7.1
Pagellus natalensis	9.1	8.6	2.9	18.8	12.9	16.9	15.6	9.8	19.1	40	7.1	41.7
Scomber japonicus	9.1	14.3	43.4	6.3	3.2	9.3	15.6	5.4	6.7			
Liza richardsoni	4.5	2.9	1.7				6.3	1.8	3.2			
Myxus capensis				6.3	3.2	18.5						
Sphyraenidae							3.1	0.9	0.1			
Totals	22	35	770.1	16	31	539.5	32	112	1825.9	5	42	91.2

3. In the field L. amia have been seen charging directly through schools of fish (pers.obs.) although murky water prevented close observations. Attack behaviour appeared to be similar to that observed in K. pelamis (see below).
4. Observations of L. amia patrolling the backline of waves strongly suggest that they hunt here. The predator would have an advantage here in surprising prey orientating to the surge or dislodged by breaking waves. Such orientation by fishes is common and has been documented by Popper & Fishelson (1973) studying Anthias squamipinnis. In the surf-zone potential prey species either orientate to maintain position or use the wave force to move to a different site. The predator could also increase its acceleration using the wave surge and the bubbles formed by breaking waves may provide a curtain behind which predators could advance undetected.

It is therefore clear that L.amia has a behavioural repertoire wide enough to take abundant schooling fishes and yet specialised enough to take prey close inshore.

Discussion

The elongate body, but strong and deep dorsal and anal fins appear to be features which provide the speed needed to outswim pelagic prey, yet allow rapid turning and manoeuvering in the surf zone and near reefs. These functions would be additional to stabilisation, attributable to the spined dorsal, and braking (Gosline 1971). A deep tail and small anterior depth and area are optimal for steady swimming, but for turning and acceleration, body area should be maximised by a greater depth along the whole body length (Webb 1977, Webb & Keyes 1981). Controlled dorsal and anal fin extension provides the most suitable profile for swimming activity (Webb 1977, Webb & Keyes 1981).

The prey taken by L. amia varies with predator size and locality. Smale & Kok (in prep.) found that juvenile L. amia (<100 mm) took small crustaceans which contributed 32.2% and 12.5% by mass of the diet in the Knysna and Swartvlei estuaries respectively. The importance of crustaceans to larger (107 - 329 mm) specimens declined, making up 4.5% and 2.7% of the diet by mass respectively. Small schooling fishes such as Hepsetia breviceps, Gilchristella aestuarius and juvenile Spondyliosoma emarginatum as well as slow moving gobies become more dominant in larger (107 - 329 mm) fish. Blaber (1973) recorded the stomach contents of 14 L. amia in West Kleinemond Estuary in the eastern Cape and prey taken were largely mullet, Gilchristella aestuarius and a single Rhabdosargus holubi. Observations by Coetzee (1982) on leervis of 100 to 800 mm in Swartvlei conformed well with both these findings, Gilchristella aestuarius, juvenile Rhabdosargus holubi and Gobiidae being important fish prey. He too found that crustaceans, especially the carid Palaemon pacificus were important. Whitfield & Blaber (1978) recorded Thryssa vitrirostris, Rhabdosargus sarba and Mugilidae in the stomachs of leervis of 120 - 782 mm in the turbid estuarine waters of Lake St Lucia. Their studies show that small schooling prey are preferred in estuarine systems, although small benthic fish and crustaceans are also important.

In the marine environment, different prey species are taken but they are largely pelagic or schooling demersal species. Lasiak's (1982) study of intertidal fishes in Algoa Bay provided information on L. amia, which had taken P. saltatrix, T. trachurus and S. ocellata. These were also recorded in the current programme. The more comprehensive sample collected during this study showed a trend for larger predators to take bigger prey although the spread of the data was partly attributable to opportunistic predation on highly abundant, relatively small schooling prey such as clupeids and engraulids. Although similar prey were taken by the two size groups of leervis, different proportions resulted in the prey being only 39% similar. The similarity of prey species taken suggests that food resource partitioning may be effected through size selection, as small predators are unable to take very large prey.

Family: Pomatomidae   Pomatomus saltatrix (Linnaeus, 1758).
Common name: elf

Description

Adults have elongate, laterally compressed bodies with two dorsal fins, the first short and low, the second longer and higher (Fig. 3, fold-out under back cover). The caudal peduncle is stout and caudal fin forked. The head is large with a large mouth, armed with a single series of strong sharp teeth. The body depth is between 22-28% of the fork length and increases to 33-38% with the dorsal and anal fins erect. The body is green-grey dorsally and pale to silvery below. Elf attain over 1 m FL and 10 kg.

Distribution

P. saltatrix is widely distributed on the eastern coast of North and South America, the west coast of Africa, the south and east coasts of Africa as far north as Mozambique, the Mediterranean and Black Sea, the north, east and south coasts of Madagascar, Australia, Tasmania, the west coast of New Zealand and in Indonesia and Malaysia (van der Elst 1976).

Habitat

P. saltatrix is normally encountered in shallow coastal waters, often close to reefs and islands, but also in the surf zone of open beaches. Juveniles and adults enter estuaries (Wallace & van der Elst 1975, van der Elst 1976, Marais & Baird 1980a,b, Lasiak 1982, Smale & Kok in prep.).

A trawling survey of south and east Cape coast fishes in 1980 (Wallace et al. in prep., Smale in prep.) revealed an extensive nursery of elf in shallow marine waters. Lasiak (1982) found elf between 70 - 508 mm TL in the intertidal region of King's Beach, Algoa Bay. Adult fish are known to move offshore to breed in Natal (van der Elst 1976), but the details of their movement and their range offshore is not yet clear.

Material

As total of 2639 P. saltatrix of 120 - 700 mm was collected (Fig.8). They were caught by hook and line or with artificial lures by fishermen, except for 10 which were collected by seine nets near the harbour

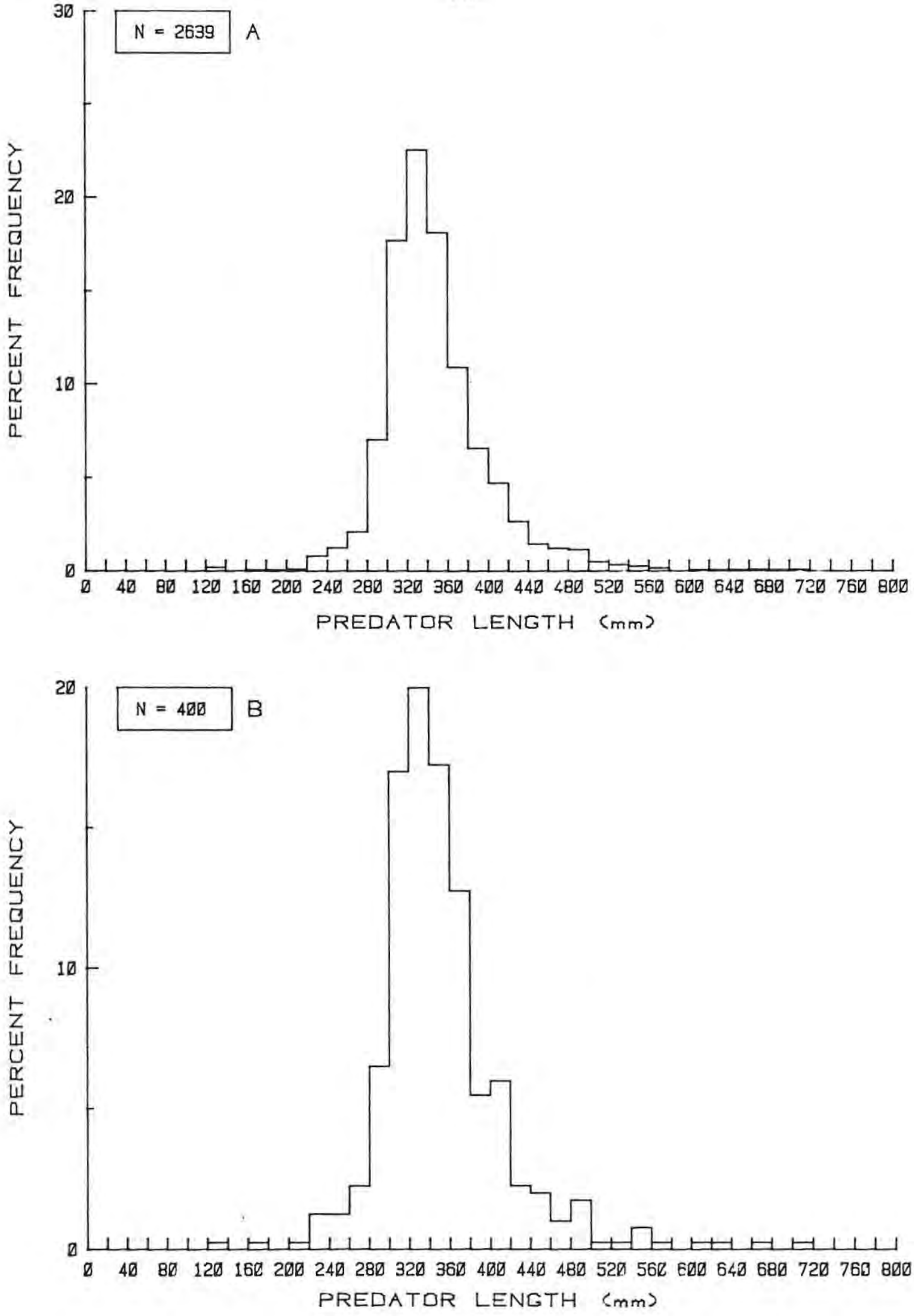


Fig. 8. Histograms of the total sample of Pomatomus saltatrix (A) and those with stomach contents (B).

breakwater, Algoa Bay. As this subsample had the same prey spectrum (Etrumeus teres, Loligo reynaudi, Trachurus trachurus and Sarpa salpa) as the fishermen's catches, the material was combined.

Regurgitation was frequently observed but difficult to quantify. A total of 400 fish ranging between 130 and 700 mm FL had prey remains in their stomachs. All elf stomachs were collected from Algoa Bay and its environs except for two from East London and one from Tsitsikamma National Park. The fullest stomach recorded in this study was 11% of the predator mass. Reconstituted stomach contents up to 70% of predator mass were recorded in this study and resulted from squid beak retention.

Feeding

The prey of P. saltatrix is presented according to predator size groups in Table 4. Groups were established after preliminary examination of their prey and the number of available samples were considered.

Principal prey are shown graphically in Fig. 9. Small fish (100 - 300 mm) took mysids (Mesopedopsis slabberi was the only species identified) occasionally (8%) but in high numbers (79% of the total number of prey), although their percentage mass contribution was low (1%). Penaeids made up 0.4% of the number and 0.1% of prey mass. The pelagic schooling squid L. reynaudi was important by mass, frequency and number (30%, 19% and 4% respectively). Pelagic schooling teleosts contributed markedly by mass (44%) although less by number and frequency. The most important species for all size groups were S. ocellata, Engraulis capensis and Etrumeus teres. Demersal schooling species contributed little (9% by mass, 2% by number). Species in this group were P. olivaceum and S. salpa. The high incidence of unidentified teleosts was attributable to post larvae and juveniles, which could not be identified owing to their small size and undifferentiated otoliths. Furthermore, prey were not always entire and sometimes only parts of the body were found in the stomachs, which often prevented their identification.

The 301 - 400 mm group took crustaceans to an insignificant extent (0.2% by mass). L. reynaudi was the single most important species by mass and the second most important by number and frequency (37%, 26% and 29% respectively). Pelagic schooling teleosts dominated the prey,

Table 4. The prey of *Pomatomus saltatrix* according to size. The totals are numbers of stomachs (F), number of items (N) and prey wet moss (M),g.

	100 – 300 mm			301 – 400 mm			401 – 500 mm			501 – 700 mm			100 – 700 mm		
Predator size group	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA															
Unidentified crustaceans				0.3	0.3	<0.1							0.3	0.2	0.1
Mysidacea	7.5	78.9	1.0	0.3	0.3	<0.1							1.3	31.4	0.1
Penaeidea	1.9	0.4	0.1	1.0	1.6	0.1							1.0	0.9	0.1
Callianassa sp				0.3	0.3	0.1							0.3	0.2	0.1
MOLLUSCA															
Loligo reynaudi	18.9	3.9	29.9	29.3	26.4	37.2	18.0	20.7	28.4				25.8	16.5	31.4
OSTEICHTHYES															
Unidentified fish	35.8	7.4	16.0	36.6	33.5	17.3	36.0	31.0	12.8	20.0	18.2	2.4	36.0	22.7	14.9
Etrumeus teres	11.3	2.7	11.9	5.9	6.5	6.9							5,8	4.3	4.9
Sardinops ocellata	11.3	2.3	18.4	17.4	17.4	25.8	22.0	19.0	25.7	10.0	18.2	13.8	17.0	11.6	24.3
Engraulis capensis	11.3	2.3	12.0	6.6	7.8	4.7	4.0	3.4	2.4				6.8	5.1	4.2
Scomberesox saurus				0.7	0.6	0.9							0.5	0.3	0.5
Cynoglossus capensis							2.0	1.7	0.1				0.3	0.2	<0.1
Chirodactylus brachydactylus				0.3	0.3	0.6							0.3	0.2	0.4
Trachurus trachurus	1.9	0.4	1.3	2.4	2.2	3.7	2.0	1.7	3.3				2.3	1.4	3.2
Pomatomus saltatrix							2.0	1.7	5.9				0.3	0.2	1.3
Argyrosomus hololepidotus				0.7	0.6	1.5	2.0	1.7	0.2				0.8	0.5	1.0
Pomadasys olivaceum	2.0	0.4	0.7	1.0	0.9	0.6	8.0	6.9	7.6	10.0	9.1	6.7	2.3	1.4	2.7
Sparidae				0.3	0.3	0.2	4.0	3.4	4.0				0.8	0.5	1.0
Boopsoidea inornata										10.0	9.1	3.2	0.3	0.2	0.3
Diplodus sargus										20.0	18.2	21.3	0.5	0.3	1.9
Pagellus natalensis				0.3	0.3	0.1	4.0	3.4	1.1				0 8	0.5	0.3
Pterogymnus laniarius										10.0	9.1	36.6	0.3	0.2	3.3
Rhabdosargus holubi				0.3	0.3	0.4							0.3	0.2	0.3
Sarpa salpa	3.8	1.2	8.6										0.5	0.5	0.5
Spondyliosoma emarginatum							4.0	5.2	8.6	20.0	18.2	16.1	1.0	0.8	3.4
Scomber japonicus				0.3	0.3	0.1							0.3	0.2	<0.1
Totals	53	256	149.1	287	322	1750.4	50	58	630.8	10	11	254	400	647	2784.3

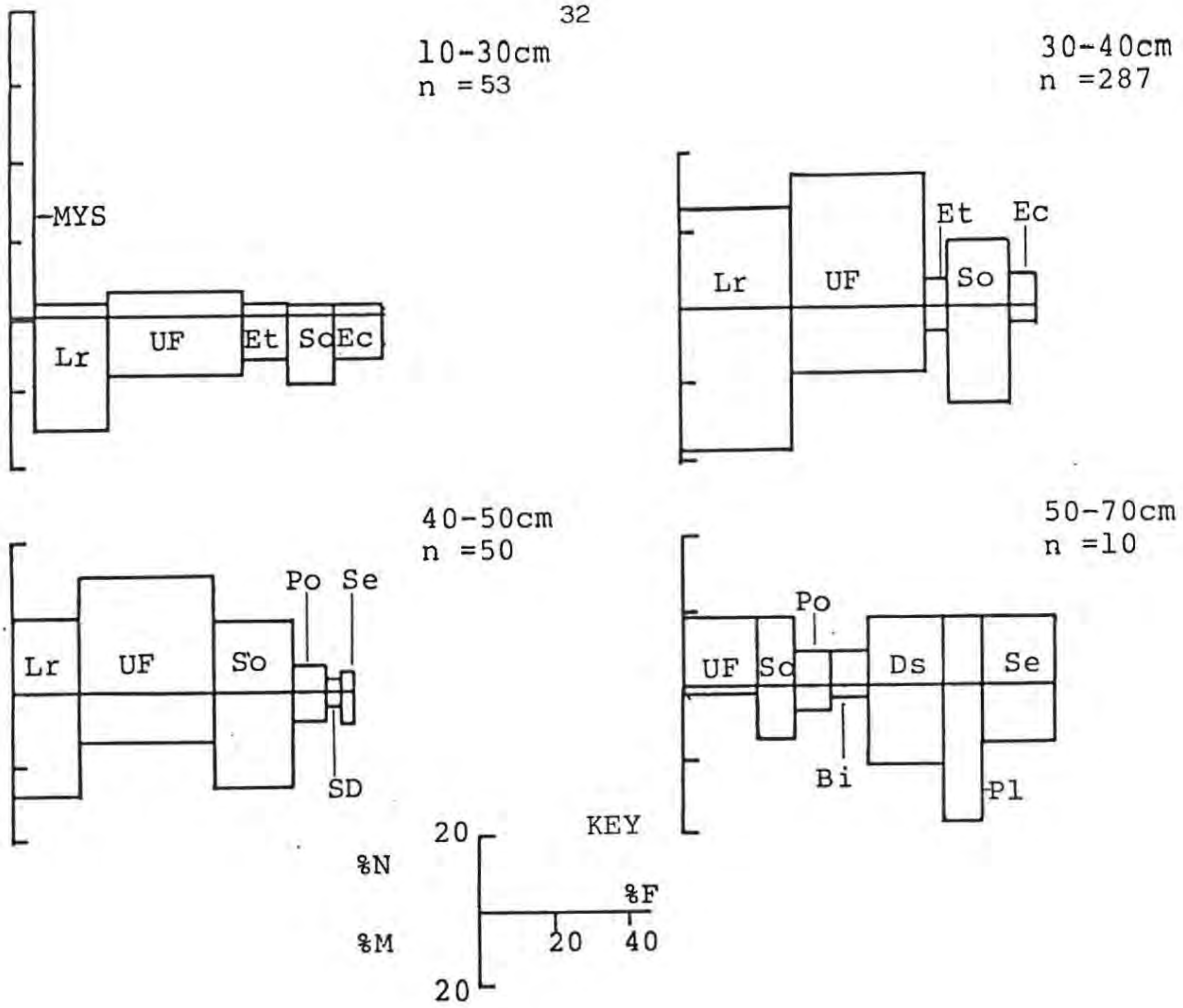


Fig. 9. Principal prey of Pomatomus saltatrix.

Bi:Boopsoidea inornata Ds:Diplodus sargus Ec:Engraulis capensis
Et:Etrumeus teres Lr:Loligo reynaudi MYS:Mysidacea Pl:Pterogymnus laniarius
Po:Pomadasys olivaceum Se:Spondyliosoma emarginatum So:Sardinops ocellata
UF:Unidentified fish.

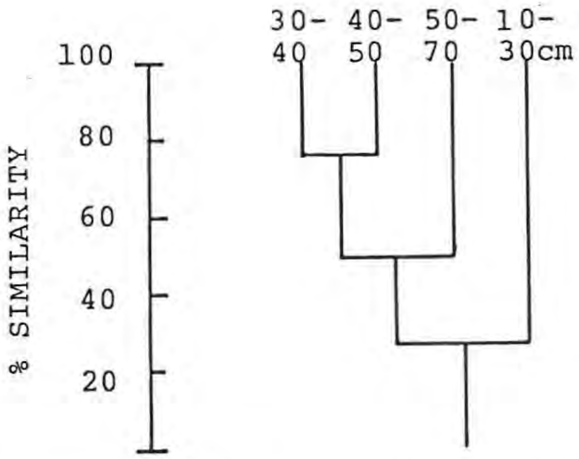


Fig. 10. Similarity dendrogram of diets of Pomatomus saltatrix size groups, according to prey mass.

representing 42% by mass and 35% by number of prey taken. Demersal species made a small contribution (3% by mass, 3% by number). Unidentified teleosts made a large contribution by frequency, number and mass (37%, 34% and 17%). Fish in the 401 - 500 mm group had taken no crustaceans. L. reynaudi was a major prey species (28% by mass, 21% by number, 18% by frequency). Unidentified teleosts were again well represented (36%F, 31%N, 13%M). Pelagic schooling teleosts were major prey (37%M and 26%N) whilst demersal species made up the balance (22%M and 22%N).

Although only 10 fish over 500 mm were recorded, the prey of this group was different from that of other groups. No L. reynaudi were recorded, although this could have resulted from the small sample size. Unidentified teleost remains were less important in this size group (20%F, 18%N, 2%M). Pelagic schooling species made up a low proportion of the diet (18%N, 14%M) whereas demersal species made up the bulk of the diet (64%N and 84%M). The latter were both species which form large schools (such as P. olivaceum) and species which occur in small groups (such as D. sargus). The group-average similarity by prey mass of the P. saltatrix size group is shown in Fig. 10.

In summary, the prey species over the size range examined are similar. Schooling pelagic species are the principal prey of all but the very large group (>500 mm), which tends to take a higher proportion of grouped demersal species. Furthermore, the smallest group took a large number of mysids but not as frequently as they took teleosts and squid. Crustaceans were not represented in the diet of P. saltatrix larger than 400 mm FL. This behaviour is also reflected when the number of prey per stomach is examined. From a high of 4.8 in the 100 - 300 mm group, the average is between 1.1 and 1.2 in larger fish. This is attributable to the change in diet from one including crustaceans to one in which single prey are usually taken.

Predator-prey length relationship

A scatter diagram of predator length against prey length is shown in Fig. 11. There is a rapid increase in maximum prey size in elf between 200 mm to 310 mm. There is an inflection point in the maxima values at about 310 mm after which there is little increase in maximum prey size. Lengths of

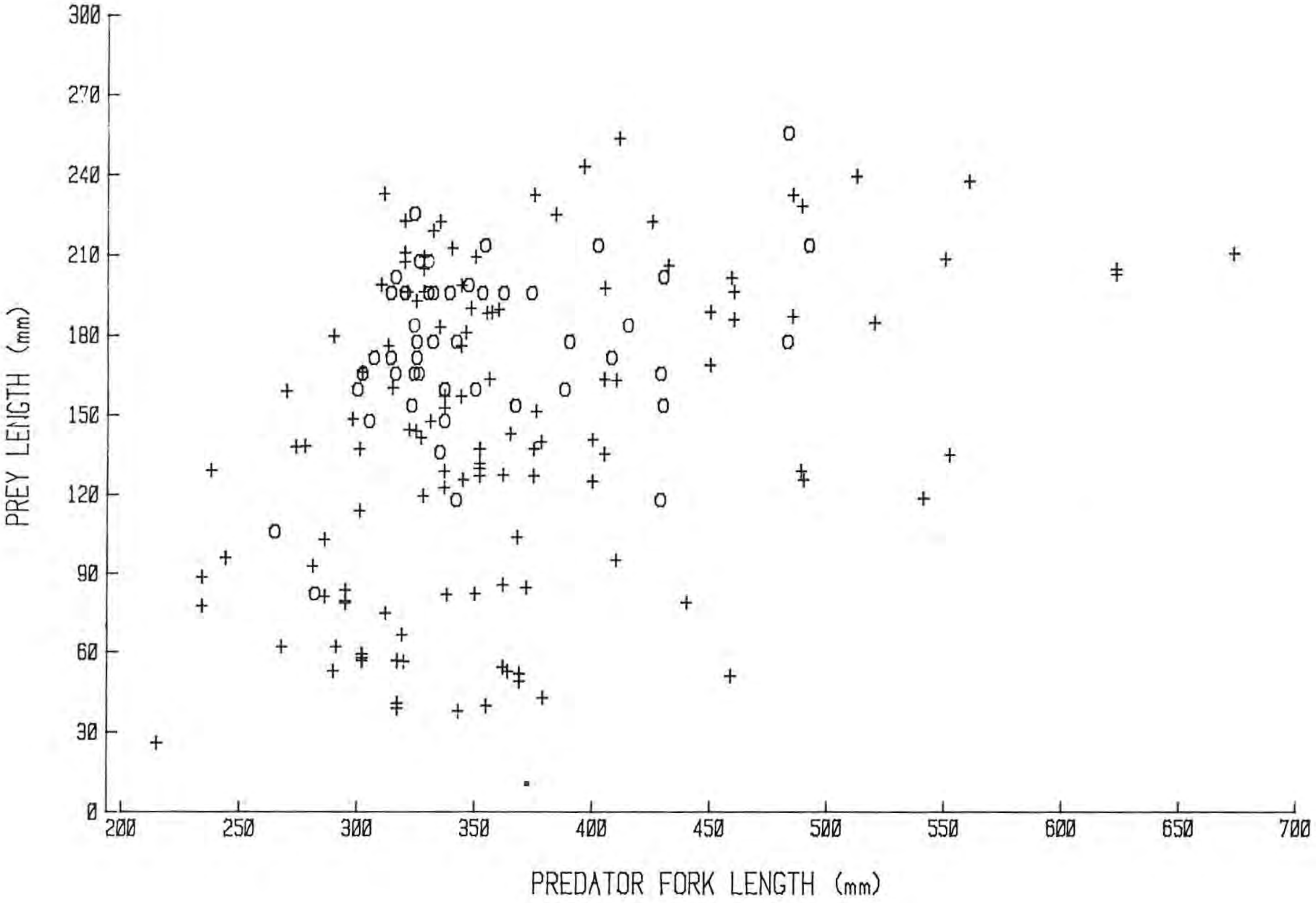


Fig. 11. Scatter diagram of prey length against fork length of Pomatomus saltatrix. Crustaceans are shown by dots, crustaceans by circles and fishes by crosses.

prey common to small elf (<300 mm) and bigger specimens (>300 mm) are plotted in Fig. 12 to clarify size selection. The trend for large specimens to take larger prey than small predators is confirmed in the case of L. reynaudi, S. ocellata, E. teres and P. olivaceum although sample size is low for small elf. This trend is not evident with small schooling engraulids.

The minimum length of prey increases in elf larger than 400 mm. The lowest ratio recorded was 2.7% and the highest 75% of predator length. This extremely high figure resulted from parts of big prey being ingested. Examination of stomach contents revealed that the sharp cutting teeth of elf can incapacitate prey by severing parts of their bodies which are then ingested. The size of these large squid and fish was calculated from beaks and otoliths found in the stomachs. Fish and squid larger than about 270 mm do not appear to be subject to predation by elf.

In summary, elf smaller than about 300 mm FL take relatively small prey. Elf larger than 300 mm can select prey over a wide size range and appear to feed opportunistically on abundant prey.

Seasonality of prey selected

The prey taken by P. saltatrix were analysed on a bi-monthly basis to investigate seasonal changes. The results are shown in Table 5. L. reynaudi is a dominant species from September to February. S. ocellata was taken throughout the year but dominated in March-June. E. capensis occurred throughout the year but E. teres was not recorded from July-October. Few stomach contents were collected in July and August.

Annual variation

The annual variation in prey of P. saltatrix is shown in Table 6. A few of the minor prey were not recorded every year of the study, but the more important species were found throughout. A large proportion of unidentified fish dominated the diet in 1978. It is likely that a lot of these were parts of S. ocellata, which were particularly abundant in 1978. Mysids were numerous but made little contribution to prey mass. L. reynaudi and S. ocellata were the two principal species taken by number

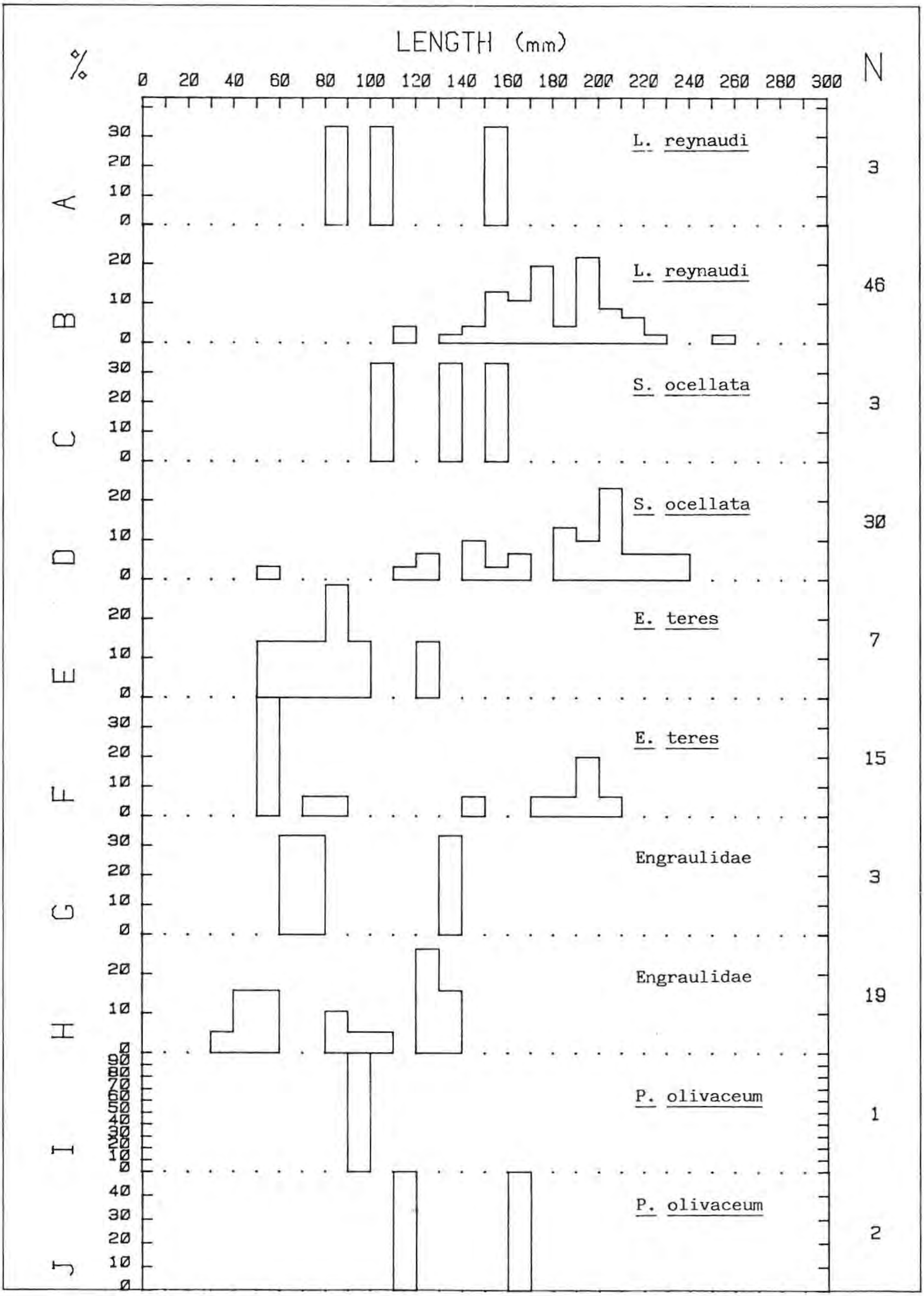


Fig. 12. Histograms of common prey of Pomatomus saltatrix <300 mm (A,C,E,G,I) and >300 mm (B,D,F,H,J,). The prey are L. reynaudi (A,B); S. ocellata (C,D); E. teres (E,F); Engraulidae (G,H) and P. olivaceum (I,J).

Table 5. Prey of *Pomatomus saltatrix* taken in bimonthly periods, all years combined. The totals are number of stomachs (F), number of items (N), and wet mass (M), g.

	January-February			March-April			May-June			July-August			September-October			November-December		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA																		
Unidentified crustaceans	0.9	0.8	<0.1															
Mysidacea				1.0	1.0	<0.1	2.0	10.7	<0.1							3.1	64.4	0.3
Penaeidea	2.8	2.5	0.1										2.7	6.8	0.5			
Callianassa sp.													2.7	2.3	1.0			
MOLLUSCA																		
Loligo reynaudi	49.5	46.2	57.8	7.2	6.7	6.9	5.9	4.6	1.6	20.0	16.7	16.8	37.8	38.6	78.7	24.0	7.6	30.9
OSTEICHTHYES Unidentified fish	27.5	25.2	11.7	40.2	38.5	19.3	27.5	23.1	12.7	30.0	33.3	6.9	45.9	38.6	9.0	42.7	13.5	21.1
Etrumeus teres	4.6	4.2	0.8	9.3	8.7	11.1	2.0	1.5	5.1							8.3	4.3	6.6
Sardinops ocellata	11.0	14.3	22.9	23.7	22.1	35.8	41.1	35.4	41.9	10.0	8.3	10.5	8.1	6.8	7.6	8.3	2.6	9.7
Engraulis capensis	2.8	2.5	0.8	8.2	7.7	2.6	12.0	12.3	2.0	10.0	8.3	6.2	2.7	2.3	1.5	8.3	4.0	14.7
Scomberesox saurus																2.1	0.7	3.3
Cynoglossus capensis				1.0	1.0	<0.1												
Chirodactylus brachydactylus							2.0	1.5	3.4									
Trachurus trachurus	1.9	1.7	0.5	2.1	1.9	2.5	2.0	1.5	7.2	10.0	8.3	0.4				3.1	1.0	9.8
Pomatomus saltatrix				1.0	1.0	4.8												
Argyrosomus hololepidotus	0.9	0.8	2.9										2.7	2.3	0.3	1.0	0.3	0.2
Pomadasys olivaceum	1.8	1.7	2.5	3.1	2.9	4.1	3.9	3.1	6.2				2.7	2.3	1.4	1.0	0.3	0.4
Sparidae				3.1	2.9	3.6												
Boopsoidea inornata										10.0	8.3	3.5						
Diplodus sargus				2.1	1.9	7.0												
Pagellus natalensis				3.1	2.9	1.0												
Pterogymnus laniarius										10.0	8.3	40.7						
Rhabdosargus holubi							2.0	1.5	2.4									
Sarpa salpa																2.1	1.0	2.8
Spondyliosoma emarginatum				1.0	1.0	1.3	3.9	4.6	17.5	10.0	8.3	14.9						
Scomber japonicus																1.0	0.3	0.2
Totals	109	119	852.9	97	104	772.2	51	65	292.1	10	12	228.5	37	44	184.2	96	303	454.4

Table 6. Annual analysis of prey taken by *P. saltatrix*. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	1978			1979			1980			1981		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Unidentified crustaceans				0.6	0.5	0.1						
Mysidacea	2.6	62.9	0.2				2.0	6.5	0.1			
Penaeidea				1.7	2.4	0.2	1.0	0.8	0.2			
Callianassa sp							1.0	0.8	0.2			
MOLLUSCA												
Loligo reynaudi	18.3	7.1	22.5	18.6	17.6	21.8	48.0	38.7	54.3	12.5	12.5	3.2
OSTEICHTHYES												
Unidentified fish	52.2	19.4	32.7	36.7	31.7	14.1	17.0	16.1	4.4	25.0	25.0	10.3
Etrumeus teres	2.6	1.0	3.6	7.3	7.3	6.6	6.0	7.3	3.8	12.5	12.5	1.7
Sardinops ocellata	14.8	5.5	15.4	23.7	23.4	38.9	8.0	7.3	4.9	12.5	12.5	63.2
Engraulis capensis	0.9	0.3	0.2	7.3	8.8	5.9	12.0	10.5	4.5	25.0	25.0	1.7
Scomberesox saurus				1.1	1.0	1.2						
Cynoglossus capensis				0.6	0.5	<0.1						
Chirodactylus brachydactylus							1.0	0.8	1.2			
Trachurus trachurus	0.9	0.3	3.6	1.7	1.5	1.7	4.0	3.2	5.4	12.5	12.5	1.1
Pomatomus saltatrix							1.0	0.8	4.3			
Argyrosomus hololepidotus	0.9	0.3	0.2	0.6	0.5	<0.1	1.0	0.8	2.9			
Pomadasys olivaceum	3.5	1.3	1.2	2.3	2.0	4.3				12.5	12.5	18.7
Sparidae	0.9	0.3	1.7	0.6	0.5	1.2	1.0	0.8	0.3			
Boopsoidea inornata							1.0	0.8	0.9			
Diplodus sargus				0.6	0.5	0.2	1.0	0.8	6.0			
Pagellus natalensis	1.7	0.6	1.2	0.6	0.5	0.1						
Pterogymnus laniarius	0.9	0.3	16.1									
Rhabdosargus holubi	0.9	0.3	1.2									
Sarpa salpa				0.6	0.5	0.4	1.0	1.6	0.9			
Spondyliosoma emarginatum				1.1	1.0	3.5	2.0	2.4	6.0			
Scomber japonicus	0.9	0.3	0.2									
Total	115	310	576.7	177	205	1273.0	100	124	857.1	8	8	77.5

and mass. In 1979 both L. reynaudi and S. ocellata were more important by number and mass, unidentified fish being a less important part of the diet. Etrumeus teres and Engraulis capensis were found in greater quantities than in 1978. In 1980 L. reynaudi dominated the prey taken.

Discussion

Pomatomus saltatrix is found along the entire South African coast (van der Elst 1981). Based on circumstantial evidence of relative abundance in anglers' catches, van der Elst (1976) hypothesized that elf move to Natal seasonally, where sexually mature fish of more than 250 mm TL are known to spawn offshore, on the Tugela Bank. Migration between Natal and the Cape has subsequently been confirmed during a large tagging programme in both areas (van der Elst, pers.comm.).

Eggs and larvae are thought to be washed to the south-west by the Agulhas Current, the juveniles swimming inshore once they have reached the Cape waters (Heydorn et al. 1978). No other spawning grounds have yet been recorded, but it seems unlikely that the entire South African population depends on this restricted area. Elf nursery areas were expected in the Cape because few young fish were found in Natal estuaries (Wallace 1975, Wallace & van der Elst 1975). However, juveniles were found in the Knysna system (van der Elst 1976). These findings have subsequently been confirmed with an increase in sampling effort in estuaries in the eastern Cape. Winter (1980) found fish of 82 mm to 310 mm in the Swartkops estuary while Smale & Kok (in prep.) found juveniles in Knysna estuary mainly in summer. A trawling survey of juvenile teleosts on the east and south Cape coasts has subsequently shown that juveniles are extremely common in the shallows (Smale in prep.). Lasiak (1982) also found elf (100-500 mm) in her study of the ichthyofauna of the surf-zone. Clearly P. saltatrix is common in the eastern Cape and must be an important predator in coastal areas.

This feeding study has shown that similar prey species are taken by P. saltatrix of 200 - 500 mm. Elf less than 300 mm, however, took smaller prey than large fish and crustaceans formed a greater proportion of the diet. Trawl data has shown that crustaceans are even more important in fish smaller than 200 mm as they make up 10 - 20% of prey by mass (Smale in prep.), although even at this size piscivory is a feature. Larvae and early juveniles were found to make up about 80% of the prey mass of elf taken by trawl.

Prey appears to vary with locality. In the surf-zone of Kings Beach, near the Port Elizabeth harbour wall, Lasiak (1982) found that elf of 100 - 500 mm took fish and cephalopods predominantly, which made up 95.8% and 3.3% of the mass. Atherina breviceps, Liza richardsoni, Pomadasys olivaceum and S. salpa were also recorded. At Bluewater Bay (near Swartkops Mouth) fish, cephalopods and Macropatasma africanum contributed 92.8%, 3.7% and 2.9% of the mass respectively. The fish identified were A. breviceps, Pagellus natalensis, Pomadasys olivaceum, S. ocellata and a mugilid. Although similar prey were recorded in Lasiak's (1982) study, the occurrence of mullet and A. breviceps which are characteristic of shallow water, suggests that prey may be taken opportunistically according to its relative abundance. Van der Elst (1976) recorded 14 teleost prey types, two crustaceans, two cephalopod taxa and incidental items in Natal. Only one fish species, P. olivaceum, was common to their diet in both studies although a species of Loligo was also noted. Despite the difference in species taken, most (12/14) were schooling, which is entirely consistant with this study. Studies outside Africa have also shown the importance of cephalopods and pelagic and demersal fish as prey of P. saltatrix. Small crustaceans are often noted prey of juveniles (Bigelow & Schroeder 1953, Grant 1962, Porumb 1968, Lux & Mahoney 1973, Richards 1976, Bade 1977).

Underwater observations by the author in Natal and the eastern Cape have shown that P. saltatrix less than 350 mm are usually seen in large schools (up to hundreds) while fish of 400 mm and larger tend to be found in smaller groups. Similar observations have been made by van der Elst (1976) who plotted length frequencies of schools caught by shore anglers. The tendency of these highly piscivorous fish to school may reduce the likelihood of cannibalism, which was noted occasionally, and is also an important factor in hunting. This has been shown by Radakov (1973) who describes interactions between elf and surmullet. It may account for the importance of obligate schooling prey in the diet of small elf which form large schools, and for the dominance of demersal prey which school in small groups in the diet of large specimens. The advantages of schooling are covered in more detail in the discussion of pelagic predators and their prey.

One distinguishing feature of elf is the sharp cutting teeth which bite through prey, as has also been observed by Bigelow & Schroeder (1953) and Lux & Mahoney (1973). Although this is not a unique feature in fish predation, it has evolved in only a few groups like the freshwater tigerfish (Jackson 1961) and piranhas (Goulding 1980). Jackson notes that tigerfish prey are usually ingested whole although Kok (1980) found that pieces of flesh may be bitten off large prey occasionally. The piranhas (Serrasalmus spp.), on the other hand, use their cutting dentition much more frequently and several predators may benefit from attacking a large prey item (Goulding 1980). Among sharks, cutting dentition is a common feature (e.g. Carcharinus spp., Sphyrna spp.). This feature has two advantages: increasing the range of prey available and spreading the benefit of successful prey capture among the school. The maximum prey taken was 75% of predator length, compared with 47% for L. amia. The advantage of prey sharing seems beneficial but not a prerequisite for successful schooling because other species which school as predators do not benefit in this way. Furthermore, lone sharks will often attack large prey. Evidently cutting teeth are one of many features which make P. saltatrix a successful predator.

Laboratory studies by Olla et al. (1970) have revealed six stages in the feeding of elf. They are: initial perception; visual fixation; pursuit, capture and ingestion; feeding intention and searching movements, and satiation. During pursuit, fish of 500 - 550 mm TL increased their swimming speed from 40 - 60 cm/sec. to 80 - 100 cm/sec. when schooling broke down. The acceleration is provided by the forked caudal and the posterior location of the dorsal and anal fins (Webb & Keyes 1981). The mouth was opened when 15 - 25 cm away from prey and the opercles extended. When satiated the frequency of prey pursuit, capture success, feeding intention and searching movements were decreased. The introduction of larger prey stimulated elf to resume feeding at a greater intensity.

Bade (1977) observed P. saltatrix of 120 mm in a tank and recorded that they attack from behind, biting through large prey and ingesting the posterior part. They either left the front to drift away or returned later to eat it.

Elf have been shown to be most active during the day, when swimming speeds increase and schooling is most evident. At night the school breaks up and swimming speed decreases (Olla & Studholme 1972). However, there is strong evidence to show that this predator is most active at twilight (Olla & Studholme 1972, van der Elst 1976). The cones of the eye are prepared for light or dark vision, thus reducing the time necessary for adaptation. The selective advantage of this rhythmic pre-adaption of the eyes, which appears to be under some internal control (Olla & Marchioni 1968), greatly increases the likelihood of success when prey are encountered at twilight, a time at which predators are believed to have an advantage over prey (Hobson 1968, 1972, 1978, Major 1977). Although elf have been seen feeding throughout the day during this study, their success probably depends on prey availability and behaviour, and water clarity.

Family: Carangidae *Seriola lalandi* Valenciennes, 1833.
Common name: Cape yellowtail

Description

Adult *Seriola lalandi* have a robust elongate body which tapers posteriorly to the caudal peduncle (Fig. 3). Body depth is about 21% FL. The lateral line is curved and the caudal peduncle is narrow but robust, its width being about 4% of fork length, with a fleshy keel. The caudal fin is widely forked and fairly rigid. The head is elongate, 25% FL. Eyes are relatively small, 3% FL. The mouth is oblique and the maxilla ends anteriorly to the eye. The gape is about 7.2% FL. Several rows of fine teeth are in the jaws and the gill rakers are elongate and strong. The body is dark blue dorsally, becoming pale blue grey laterally with a yellow stripe which runs the length of the body. Ventrally it is cream-white to pale grey. It attains 150 cm and 50.3 kg (van der Elst 1981).

Distribution

S. lalandi is circumglobal and restricted to the subtropical waters of Africa, Japan, Australia, Brazil and the west coast of the United States (Smith-Vaniz & Berry 1981).

Habitat

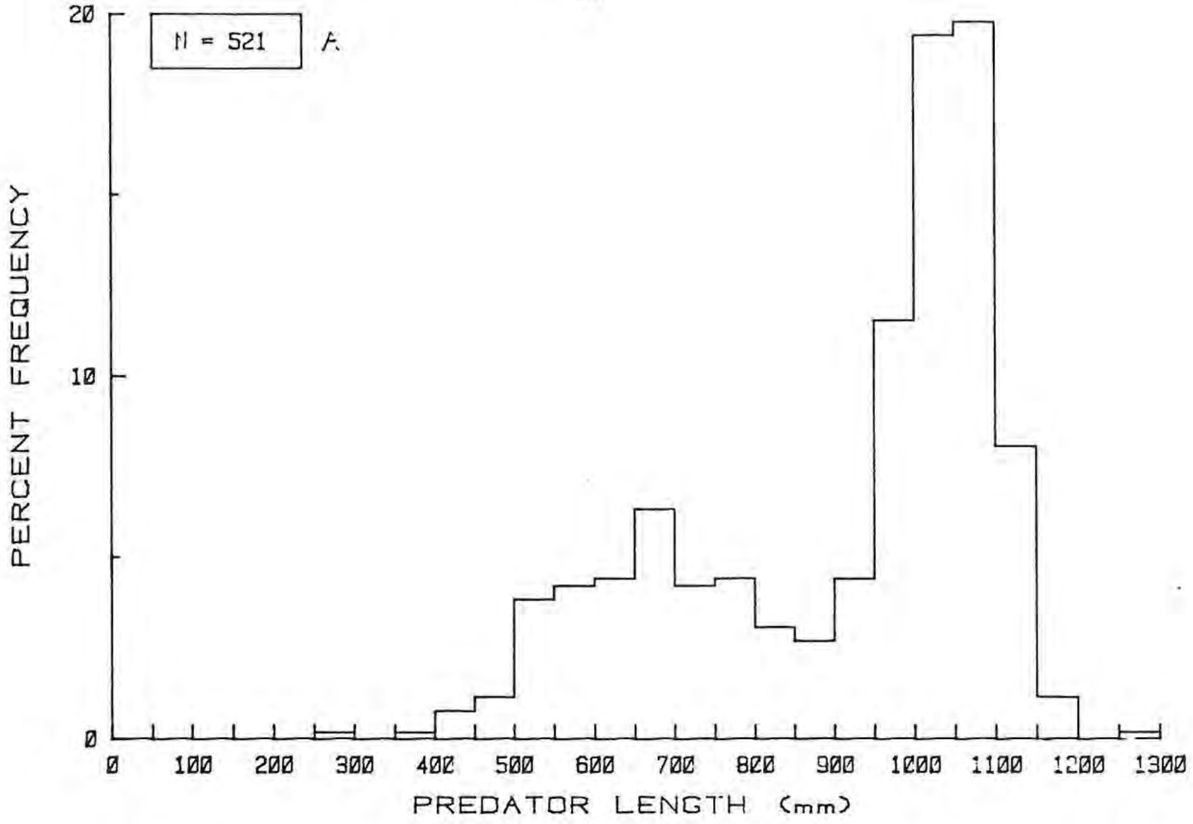
The species is most common in cooler waters. It is pelagic but is associated with pinnacles and reefs over which schools often patrol in large numbers. Only occasionally are fish seen singly. They occur in shallow water but are more common in deep water and may be found at the edge of the continental shelf. Large schools are seen apparently basking close to the surface. In the vicinity of Port Elizabeth they are frequently found at Bird Island, Riybank and over pinnacles in the Noordhoek and Sardinia Bay area (Fig. 2).

Materials

Of 521 S. lalandi sampled, 206 had prey remains in their stomachs. A subsample of 12 yellowtail were shot by speargun. They had taken Loligo reyanudi principally and also Sardinops ocellata and Trachurus trachurus. As these prey were similar to those of line-caught fish they were included in the larger sample. The length composition of the sample is shown in Fig. 13. The fullest stomach recorded in this study was 5.2% of predator mass. The highest reconstituted stomach mass was 24.8%; this resulted from marked retention of squid beaks.

Feeding

Yellowtail were divided into two size groups and the prey of each is presented in Table 7. Principal prey are shown in Fig. 14. In small S. lalandi (<700 mm FL), pelagic schooling teleosts (including T. trachurus, Sardinops ocellata, Scomberesox saurus, Petalichthys capensis, Sphyraena africanum and Scomber japonicus) formed a major component of the diet by number and mass (66%N, 74%M). Demersal teleosts were of minor importance. Boopsoidea inornata, Pachymetapon aeneum and Pagellus natalensis were equally represented by frequency and number but P. natalensis made a larger contribution by mass. Demersal teleosts made up 4% by number and 7% by mass of the diet. Unidentifiable teleosts were encountered frequently (22%) and resulted from the rapid digestion of the prey. Their contribution by number and mass was also high (17%N,



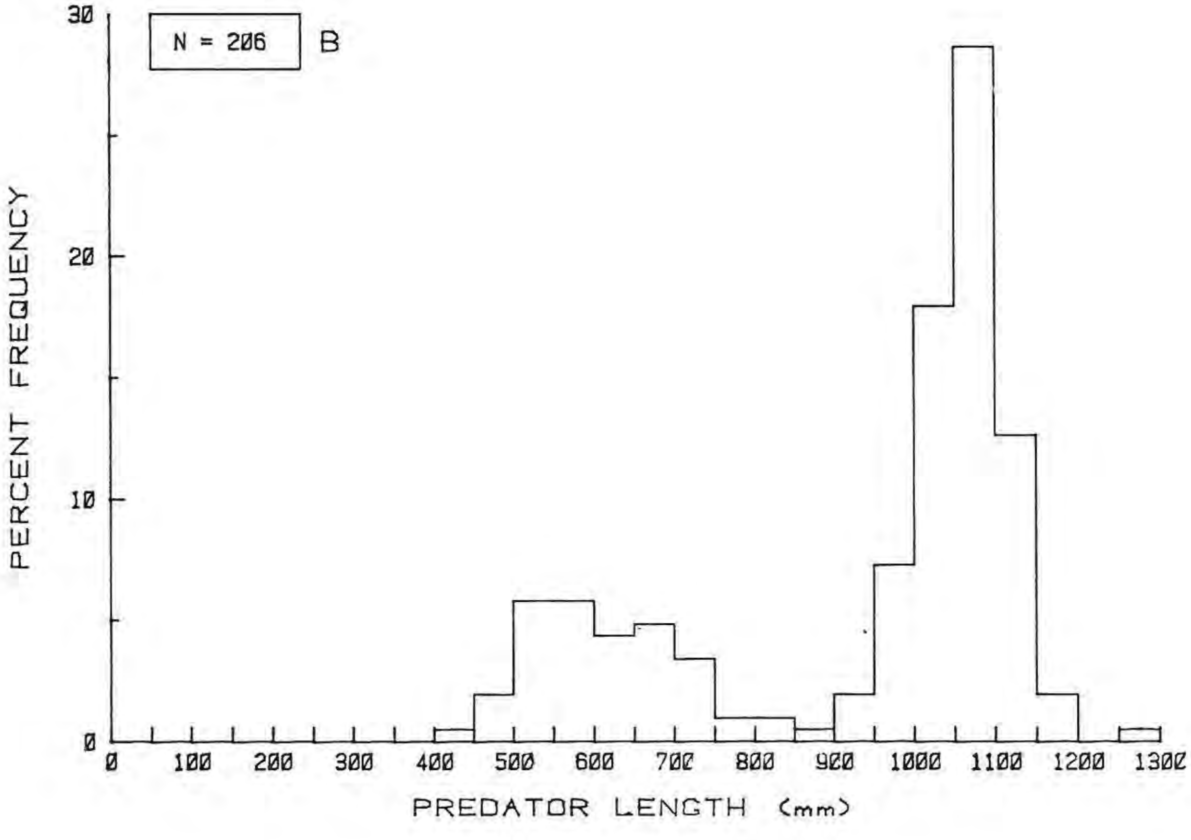


Fig. 13. Histograms of the total sample of Seriola lalandi (A) and those with stomach contents (B).

Table 7. The prey of *Seriola lalandi* according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M),g.

Prey	400 - 700 mm			701 - 1300 mm			400 - 1300 mm		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA									
Stomatopoda	10.2	7.1	0.2				2.4	1.8	<0.1
Megalopa larvae	4.1	1.6	0.1				1.0	0.4	<0.1
MOLLUSCA									
Sepiidae				2.5	1.1	0.9	1.9	0.8	0.8
Loligo reynaudi	12.2	4.7	4.5	77.7	71.7	67.2	62.1	54.5	63.8
Ommastrephidae				0.6	0.3	<0.1	0.5	0.2	<0.1
OSTEICHTHYES									
Unidentified fish	22.4	16.5	14.3	3.8	3.3	0.3	8.3	6.7	1.1
Etrumeus teres	4.1	2.4	4.9	2.5	1.1	0.9	2.9	1.4	1.1
Sardinops ocellata	16.2	13.4	29.4	12.7	14.7	18.4	13.6	14.3	19.0
Engraulidae				0.6	0.8	<0.1	0.5	0.6	<0.1
Engraulis capensis	6.1	2.4	2.6				1.5	0.6	0.1
Scomberesox saurus	6.1	5.5	7.7	0.6	0.3	0.1	1.9	1.6	0.5
Petalichthys capensis	8.2	3.2	10.4				1.9	0.8	0.6
Chirodactylus brachydactylus	2.0	0.8	1.6				0.5	0.2	0.1
Acanthistius sebastoides				1.3	0.8	1.4	1.0	0.6	1.3
Trachurus trachurus	16.3	25.2	3.5	2.5	1.4	3.7	5.8	7.5	3.7
Pomatomus saltatrix				2.5	1.1	3.1	1.9	0.8	2.9
Scombrops dubius	2.0	1.6	1.1				0.5	0.4	0.1
Argyrosomus hololepidotus				1.3	0.5	1.0	1.0	0.4	0.9
Sparidae	2.0	0.8	0.8				0.5	0.2	<0.1
Argyrozona argyrozona				0.6	0.5	0.2	0.5	0.4	0.2
Boopsoidea inornata	2.0	0.8	0.6	1.3	0.5	0.4	1.5	0.6	0.4
Pachymetapon aeneum	2.0	0.8	0.6				0.5	0.2	<0.1
Pagellus natalensis	2.0	0.8	3.5				0.5	0.2	0.2
Spondyliosoma emarginatum				1.9	0.8	0.3	1.5	0.6	0.3
Scomber japonicus	10.2	4.7	6.9	2.5	1.1	2.1	4.4	2.0	2.4
Sphyraena africanum	10.2	7.9	7.1				2.4	2.0	0.4
Totals	49	127	856.5	157	368	14855.9	206	495	15712.4

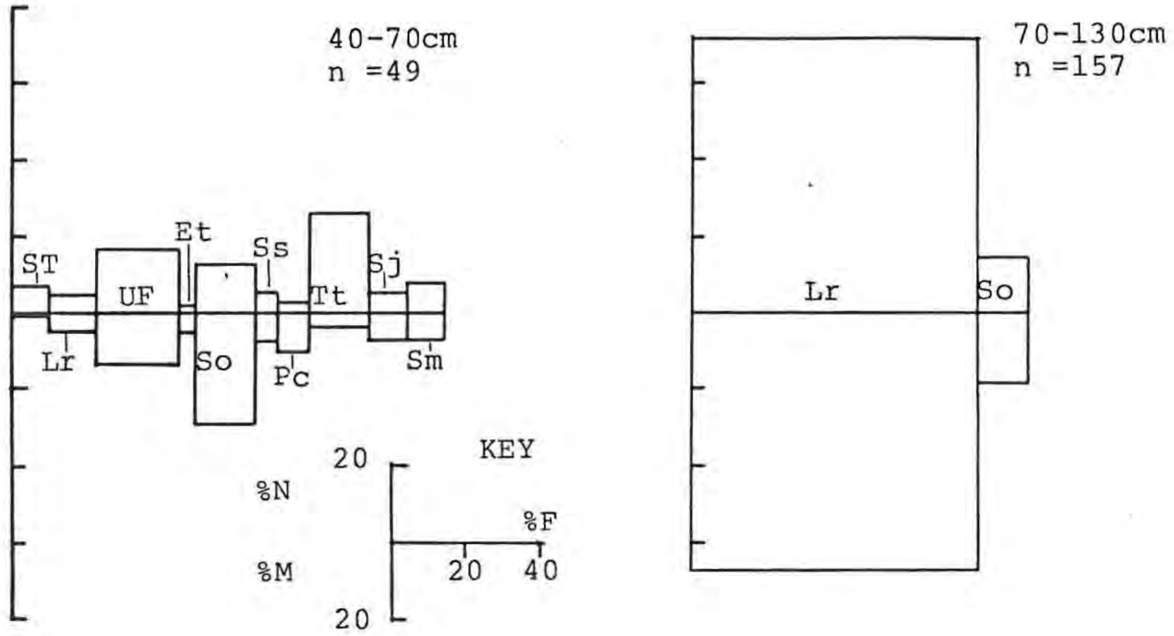


Fig. 14. Principal prey of *Seriola lalandi.*

Et:*Etrumeus teres* Lr:*Loligo reynaudi* Pc:*Petalichthys capensis* Sj:Scomber *japonicus*
Sm:*Sphyraena africanum* So:*Sardinops ocellata* Ss:*Scomberesox saurus* ST:Stomatopoda
Tt:*Trachurus trachurus* UF:Unidentified fish

14%M). Loligo reynaudi was the dominant invertebrate species which made up 5% of the diet by mass and 5% by number but 12% by frequency. Brachyuran megalopae were encountered occasionally (4%F, 2%N, 0.1%M) and stomatopoda were found in 10% of the stomachs examined and made up 7% of the number and 0.2% of the mass of prey. Thus crustaceans made up a minor proportion of the diet numerically and gravimetrically (9%N, 0.3%M).

In the large group (701 - 1300 mm) L. reynaudi dominated the diet (78%F, 72%N and 67%M). S. ocellata was the only other major prey species which, with the other pelagic teleosts, made up 21% of the number and 28% of the mass of prey taken. Demersal fishes made a small contribution to the diet (3%N, 3%M). The diets of the two size groups are 30% similar in terms of prey mass.

The average number of prey found in the stomachs of small and large S. lalandi was very similar (2.6 and 2.3 respectively). However, the large size group often had the remains of squid beaks and gladii from which most or all of the flesh had been digested. Retention of these digestion-resistant parts tends to over-emphasize the number of prey taken per unit time as accumulation may occur over several hours and possibly days. The small size group thus takes a larger number of prey on average than do large specimens.

Predator-prey length relationship

The relationship between S. lalandi and the prey length is expressed in Fig. 15. A wide size range of prey is taken, the maximum was 67% and the minimum 7%. The extremely high values recorded in predators of 500 - 700 mm are caused by the presence of the very elongate species, Petalichthys capensis, in the diet. Without these, a more gradual increase would be obtained and the curve of maximum values would level off after about 800 mm. Only one L. reynaudi was measured from small yellowtail (<700 mm), but it was a dominant prey of larger fish. The squid were 7-37% of predator length.

Lengths of prey taken commonly by both size groups of S. lalandi are plotted in Fig. 16. The size of L. reynaudi and S. ocellata is very similar in both size groups, but big yellowtail took larger S. saurus, T. trachurus and S. japonicus than did small S. lalandi. However, the

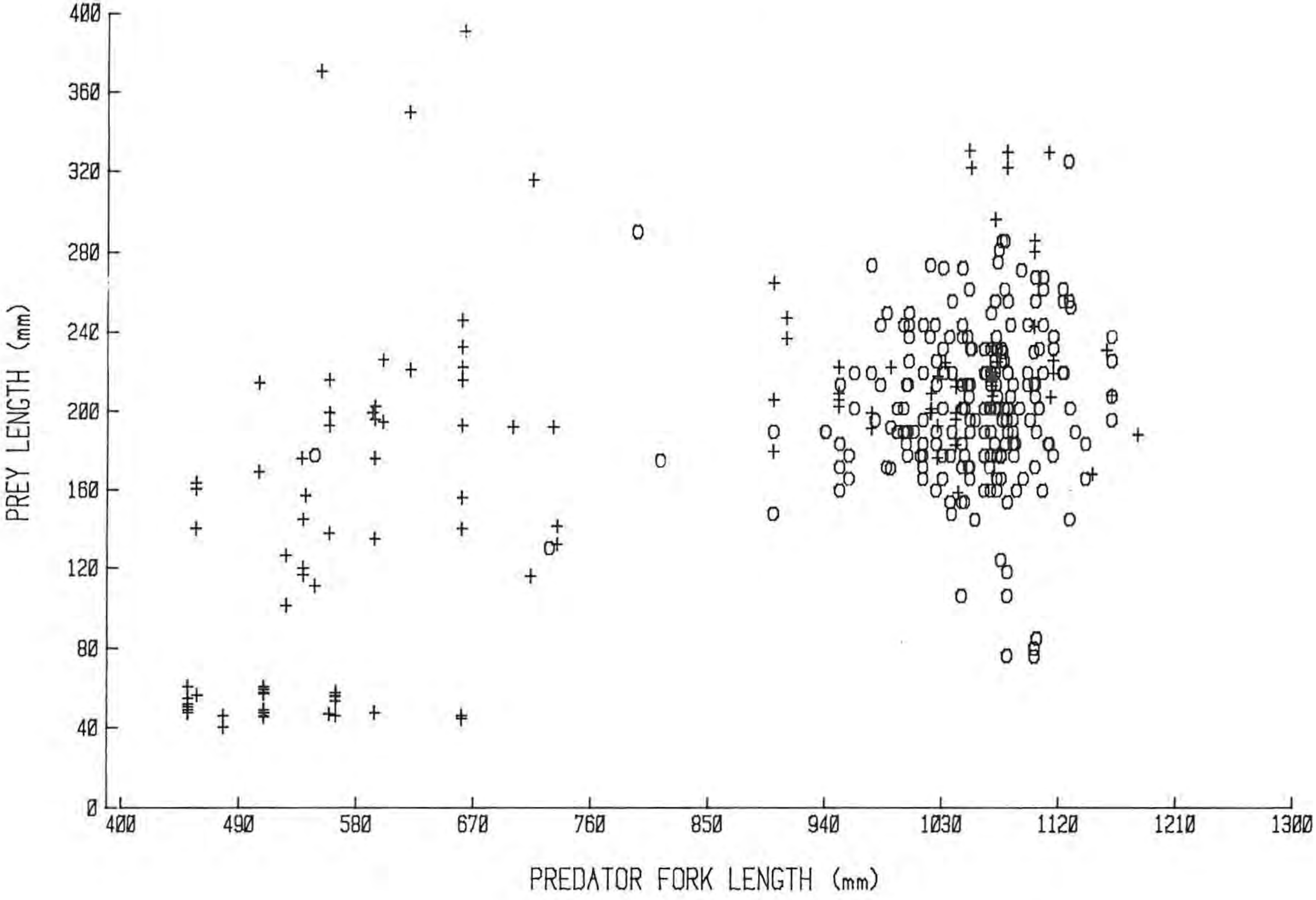


Fig. 15. Scatter diagram of prey length against fork length of Seriola lalandi. Cephalopods are shown by circles and fishes by crosses.

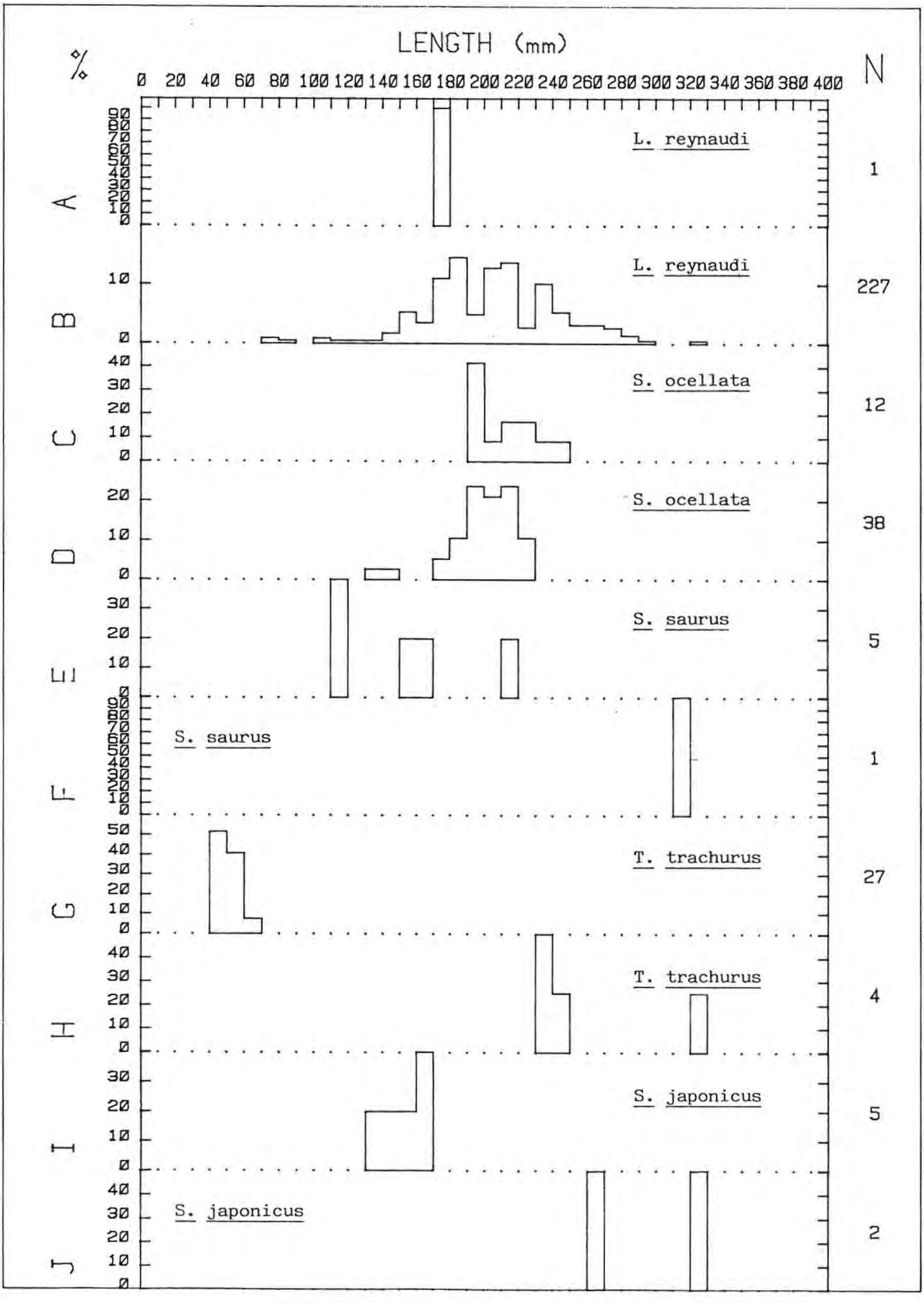


Fig. 16. Histograms of common prey of Seriola lalandi < 700 mm (A,C,E,G,I,) and > 700 mm (B,D,F,H,J). The prey are : L. reynaudi (A,B); S. ocellata (C,D); S. saurus (E,F); T. trachurus (G,H) and S. japonicus (I,J).

smaller group took Petalichthys capensis of 328-390 mm (not shown in Fig.16), which shows that elongate and thin prey are taken by large and small predators.

Seasonality of prey selected

The two size groups of S. lalandi were maintained during an analysis of the seasonality of prey selected. This was done because earlier analysis of prey selection revealed large differences in the species taken by these two groups. Results are presented in Table 8. Small yellowtail (401 - 700 mm) took different species of prey sporadically through the year. This is probably attributable to the small sample available. In January-February S. ocellata and T. trachurus were important prey while E. teres and P. capensis are more dominant in May-June. Although only five yellowtail were collected in September-October the importance of two sparids and unidentified fish may result from schooling pelagic prey moving away. P. capensis, S. saurus and S. africanum dominate in November-December by mass. L. reynaudi is also an important prey species in these two months.

Yellowtail of 701 - 1300 mm took squid (L. reynaudi) throughout the year, and squid dominated the diet by number and mass in every period except in September-October when T. trachurus was more dominant by mass. Another important species was S. ocellata, which was recorded in the first half of the year and in November-December. Other species contributed sporadically through the year.

Annual variation

An analysis of prey on an annual basis is shown in Table 9. In all years L. reynaudi dominated the prey by number and mass, showing an increased dominance with time. In 1978 Sardinops ocellata was the most important of the teleosts taken but declined in importance with time, becoming insignificant in 1980. Some species were recorded at low levels throughout the study (E. teres and Scomber japonicus). Others were recorded over only one or two years of the study (e.g. Scomberesox saurus, Trachurus trachurus).

Discussion

Seriola lalandi is widely distributed. Smith-Vaniz & Berry (1981) consider S. dorsalis, S. papei and S. banisteri to be junior synonyms of

Table 8 (a) The prey of Seriola lalandi of 400 - 700 mm taken in bi-monthly periods, all years combined. The totals are number of stomachs (F), number of items (N) and prey wet mass (M),g.

	January-February			March-April			May - June			July-August			September-October			November-December		
Prey species	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA																		
Stomatopoda							20.0	50.0	1.7				80.0	21.1	8.5			
Megalopa larvae				8.3	7.7	0.3							20.0	5.3	2.3			
MOLLUSCA																		
Loligo reynaudi	12.5	3.2	1.7													36.4	18.2	13.9
OSTEICHTHYES																		
Unidentified fish				66.7	61.5	59.6	20.0	10.0	8.5				40.0	63.2	12.3			
Etrumeus teres	6.3	1.6	2.8				20.0	20.0	54.2									
Sardinops ocellata	43.8	25.4	63.7	8.3	7.7	13.9												
Engraulis capensis	18.8	4.8	6.4															
Scomberesox saurus																27.3	31.8	27.9
Petalichthys capensis	6.3	1.6	1.7				40.0	20.0	35.6							9.1	4.5	26.2
Chirodactylus brachydactylus				8.3	7.7	7.2												
Trachurus trachurus	50.0	50.8	8.6															
Scombrops dubius																9.1	9.1	3.8
Sparidae				8.3	7.7	3.6												
Boopsoidea inornata													20.0	5.3	38.5			
Pachymetopon aeneum													20.0	5.3	38.5			
Pagellus natalensis				8.3	7.7	15.4												
Scomber japonicus	25.0	7.9	12.9													9.1	4.5	5.9
Sphyraena africanum	12.5	4.8	2.3													27.3	31.8	22.4
Totals	16	63	353.2	12	13	194.5	5	10	59				5	19	13	11	22	236.8

Table 8 (b) The prey of *Seriola lalandi* of 701 -1300 mm taken in bi-monthly periods, all years combined. The totals are number of stomachs (F), number of items (N) and prey wet mass (M),g.

	January-February			March-April			May-June			July-August			September-October			November-December		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA																		
MOLLUSCA																		
Sepiidae				1.6	0.7	<0.1	5.4	2.5	0.8	14.3	4.2	23.9						
Loligo reynaudi	45.5	57.1	87.7	72.1	63.3	58.6	81.1	71.6	58.3	71.4	58.3	59.2	66.7	76.9	39.6	94.7	94.9	95.3
Ommastrephidae				1.6	0.7	<0.1												
OSTEICHTHYES																		
Unidentified fish	9.1	4.8	0.5	1.6	0.7	0.1	5.4	2.5	0.6	14.3	29.2	2.6	33.3	7.7	0.8			
Etrumeus teres	9.1	4.8	1.3	4.9	2.0	1.6												
Sardinops ocellata	27.3	23.8	6.9	19.7	23.3	26.2	5.4	12.3	22.4							7.9	5.1	4.7
Engraulidae							2.7	3.7	0.1									
Scomberesox saurus							2.7	1.2	0.3									
Acanthistius sebastoides				1.6	1.3	0.5	2.7	1.2	5.7									
Trachurus trachurus				4.9	2.0	4.6							33.3	15.4	59.6			
Pomatomus saltatrix	9.1	4.8	2.4	1.6	0.7	3.2	5.4	2.5	7.0									
Argyrosomus hololepidotus				3.3	1.3	2.1												
Argyrozona argyrozona				1.6	1.3	0.4												
Boopsoidea inornata	9.1	4.8	1.3							14.3	4.2	7.9						
Pachymetopon aeneum																		
Spondyliosoma emarginatum				3.3	1.3	0.2				14.3	4.2	6.4						
Scomber japonicus				3.3	1.3	2.4	5.5	2.5	4.8									
Totals	11	21	1344.9	61	150	7053.2	37	81	2970.0	7	24	456.3	3	13	389	38	79	2642.5

Table 9. The prey *Seriola lalandi* taken in different years of the study. The totals are number of stomachs (F), number of items (N) and prey wet mass (M),g.

	1978			1979			1980			1981		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Stomatopoda	7.8	5.7	0.1									
Megalopa larvae	3.1	1.3	<0.1									
MOLLUSCA												
Sepiidae	1.6	0.6	0.3	1.3	0.6	1.6	4.2	2.0	0.3			
Loligo reynaudi	42.2	43.3	46.7	77.3	72.9	66.5	83.3	74.3	76.8	15.8	4.5	30.5
Ommastrephidae							2.1	1.0	0.1			
OSTEICHTHYES												
Unidentified fish	23.4	19.7	4.4	1.3	0.6	0.1				5.3	1.5	1.3
Etrumeus teres	1.6	0.6	0.9	1.3	0.6	0.2	6.3	4.0	2.4	5.3	1.5	1.9
Sardinops ocellata	18.8	17.8	39.6	9.3	12.9	17.9	2.1	2.0	1.9	42.1	28.4	45.3
Engraulidae							2.1	3.0	0.1			
Engraulis capensis										15.8	4.5	4.3
Scomberesox saurus	1.6	0.6	0.3	4.0	4.1	1.0						
Petalichthys capensis				4.0	1.8	1.2				5.3	1.5	1.1
Chirodactylus brachydactylus	1.6	0.6	0.4									
Acanthistius sebastoides				1.3	0.6	2.5	2.1	2.0	0.7			
Trachurus trachurus				2.7	1.8	6.9	4.2	2.0	1.8	42.1	47.8	5.8
Pomatomus saltatrix				1.3	0.6	0.5	6.3	3.0	9.2			
Scombrops dubius	1.6	1.3	0.2									
Argyrosomus hololepidotus							4.2	2.0	3.1			
Sparidae				1.3	0.6	0.1						
Argyrozona argyrozona							2.1	2.0	0.6			
Boopsoidea inornata	3.1	1.3	1.1	1.3	0.6	0.2						
Pachymetopon aeneum	1.6	0.6	0.1									
Pagellus natalensis				1.3	0.6	0.4						
Spondyliosoma emarginatum	1.6	0.6	0.8				4.2	2.0	0.4			
Scomber japonicus	3.1	1.3	3.6	2.7	1.2	1.0	2.1	1.0	2.9	21.1	7.5	8.7
Sphyraena africanum	4.7	4.5	1.5	1.3	0.6	<0.1				5.3	3.0	1.1
Totals	64	157	3614.5	75	170	6884.5	48	101	4688.2	19	67	525.2

S. lalandi. In South Africa *S. lalandi* is found along the Cape south coast from October to March in large shoals. They are found in Natal from July to September (Penny, Sea Fisheries Institute, pers.comm., pers.obs.), strongly suggesting a north-easterly migration in winter. These observatioons correspond with the seasonal occurrence of large *S. lalandi* shoals in the eastern Cape, although they may be caught intermittently through the year. The reason for migration in south African waters needs further investigastion although van der Elst (1981) stated that spawning has been recorded off the Natal coast. Baxter (1960) also noted long migrations along the California coast, most of the fish having migrated there from central Baja, California. Penny (pers.comm.) believes that the major spawning area is in the southern Cape off Cape Agulhas. This clearly needs further investigation, as no clear evidence was obtained during a local study (Smale in prep.).

Anatomically, *S. lalandi* is ideally suited to sustained swimming, which would facilitate efficient migrations. It has a deeply forked tail, a narrow caudal peduncle and an elongate torpedo-shaped body. Its caudal fin is used for low-speed cruising and it swims in a carangiform mode according to Webb & Keyes (1981). The mean cruising speed of 10 fish of 0.6 m held in captivity was 1.13 ± 0.06 body lengths/sec. (N=20) (Webb & Keyes 1981), which means that these fish could move about 30 km in 12 hours at 'cruising speed'. Their swimming speed would permit them to travel from Cape Agulhas to Natal (about 1250 km) in about 6 weeks when migrating. This estimate agrees with the time of arrival and departure of the schools in these areas (van der Elst 1981, Penny pers.comm., pers.obs.).

S. lalandi appear to outswim their prey, apparently attacking as a school, probably as a straight "charge". Webb & Keyes (1981) observed that yellowtail exhibit little turning with feeding, having to use three tail beats to negotiate a 180° turn (as opposed to 1 beat for dolpin, *Coryphaena hippurus* which is able to raise the median fins to assist manoeuvrability). In this study, *S. lalandi* was found to swim in schools of similar sized individuals and within such groups, the prey taken was almost identical. Baxter (1960) recorded the same finding for *S. dorsalis* (=*S. lalandi*) off California. Furthermore, they appear to be diurnal predators, judging by the fresh state of prey found in many stomachs, as was also recorded by Baxter (1960). The relative proportions of the principal prey species were found to change through the year, probably reflecting changes in availability of suitable food. Baxter (1960) found large changes of principal prey over a short period which made him suggest that this species is an opportunist feeder. Although yellowtail larger than 700 mm also took fishes, squid, predominantly L. reynaudi, were the principal prey. Retention of the beaks in stomachs was noted during this study, which would tend to increase the number recorded. However, both the wet mass and frequency were higher than other prey which indicates this was not a serious shortcoming. Beak retention prevented the use of reconstituted prey mass in diet analyses as this would have introduced a large bias.

Resource partitioning within the species appears to be related to prey species selection. Small yellowtail take mainly schooling fishes while large ones take L. reynaudi predominantly. Partitioning is further related to habitat use. Diving observations and discussions with experienced local fishermen indicate that the small fish school in open water, often in the shallows such as near Bird Island (Algoa Bay). Large specimens are usually found near pinnacles and close to reefs especially at Riybank and Noordhoek, where squid runs commonly occur. Baxter (1960) found that fish of ages 3 - 8 years school with others of the same size and move around extensively. Large fish of 8 years and older (>1000 mm) are seldom found in dense schools, and apparently become relatively sedentary. Although there appears to be habitat selection, this may well break down during migration when schools of large individuals move into the water column away from reefs. This clearly happens during spawning when fish move offshore (Baxter 1960). Small-scale movements of tagged yellowtail moving from bank to bank off the south Cape coast have been recorded by the Sea Fisheries Institute (Penny pers.comm.). They move varying distances between fishing grounds - in the local study this was between Cape Point and Cape Infanta. Some of the fish travelled between Cape Agulhas and Cape Point in about 4 days, giving them an overall travelling rate of roughly 35 km/d, corresponding well with cruising speed estimates made in the aquarium (Webb & Keyes 1981). These movements appeared to be related to changes in wind patterns (Penny pers.comm.) which probably influenced water currents, temperature or prey availability.

Family: Sciaenidae Atractoscion aequidens (Cuvier, 1830)
Common name: geelbek

Description

The body is elongate and robust, tapering to the thick caudal peduncle (Fig. 3). Body depth is about 20% FL and 36% with the dorsal and pelvic fins extended. The lateral line is almost straight, ending at the caudal fin. The thick caudal peduncle is not keeled and the caudal fin is lunate. The head is pointed and moderately elongate (26.5% FL). The eye is large, about 4% FL. The mouth is large, and the maxillary extends below the hind edge of the eye or beyond. The gape is about 16% FL and the jaws bear several rows of small backwardly pointed needle-like teeth but no canines. Gill rakers are short and total 12-16. The body is silvery to bronze dorsally and pale silvery ventrally with a black axillary spot at the base of the pectoral fin. The yellow mouth and inside of the gill covers are described in the common name geelbek. It attains 120 cm and 22.7 kg (van der Elst 1981).

Distribution

A. aequidens is found on the east, south and west coasts of South Africa to Angola. Trewavas (1977) records this species on the southern and eastern coasts of Australia.

Habitat

A. aequidens is a pelagic species which may be found close to shore and occurs down to 100 m. Juveniles are demersal, being found in sandy areas (Smale in prep.). Adults range widely, apparently moving up to Natal and Zululand to spawn (van der Elst 1981), although details of their life history are not yet clear. Adults are often found near pinnacles, ledges and wrecks, close to the bottom or swimming near the surface, away from reefs (pers.obs.,van der Elst 1981). They are caught almost throughout Algoa Bay, but particularly near Bird Island and off Noordhoek and Sardinia Bay. They occur sporadically and always seem to move in schools of similar sized fish.

Material

A total of 848 specimens was collected and 59 stomachs with contents were examined. The length range of the total sample varied between 283 and 992 mm. Those with stomach contents varied between 345 and 970 mm (Fig. 17). The maximum stomach fullness found was 5.9% of predator mass while the maximum reconstituted stomach mass was 19.5% of predator mass. This high value resulted from the retention of cephalopod beaks in the stomach.

Feeding

The prey of A. aequidens are listed in Table 10, and the principal prey are illustrated in Fig. 18. The smallest size-group (300 - 600 mm FL) took crustaceans (megalopa larvae) and these made up 2% of the number and 0.1% of prey mass. The only cephalopod taken was L. reynaudi which made up 7% of the prey number and 3% of the prey mass. Fish made up 91% of the prey number and 97% of the prey mass. These were largely schooling pelagic species such as S. ocellata and E. capensis (59%N, 72%M). Demersal species were less important (7%N, 19%M). Unidentified fish made up the balance (25%N, 6%M).

The larger size-group took very similar prey, but no crustaceans. The cephalopods represented were Sepiidae and L. reynaudi (7%N, 1%M). Pelagic schooling fish made up 61% of the number and 83% of the prey mass. Demersal fish contributed 14% and 7% respectively. The prey taken were very similar. A similar co-efficient of 67% was found for the diets of these two size groups, in terms of prey mass.

Predator-prey length relationship

The scatter diagram illustrated in Fig. 19 shows the relationship between predator and prey length. Prey varied between 9 and 56% of predator length. Over the size range studied there was little variation in the maximum size of prey. Small fish of less than 520 mm took smaller prey than larger predators.

Seasonality of prey selected

The limited number of stomachs collected intermittently through the years precluded meaningful analyses of temporal dietary variations.

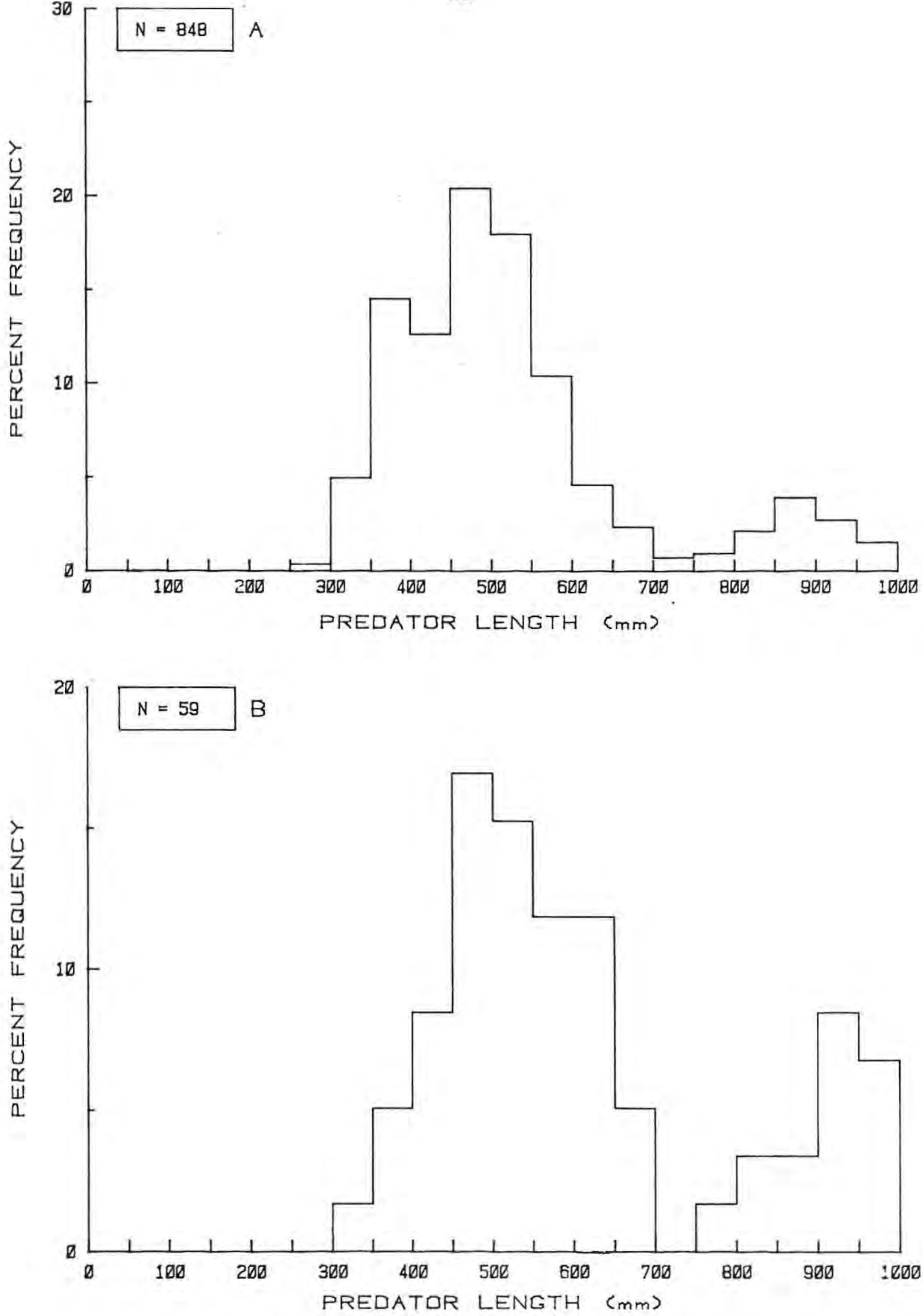


Fig. 17. Histograms of the total sample of Atractoscion aequidens (A) and those with stomach contents (B).

Table 10. The prey of <u>Atractoscion aequidens</u> according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

	300-600 mm			601-1000 mm			300-1000 mm		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA									
Megalopa larvae	2.8	2.3	0.1				1.7	1.4	<0.1
MOLLUSCA									
Sepiidae				4.3	3.6	1.0	1.7	1.4	0.6
<u>Loligo reynaudi</u>	8.3	6.8	2.8	4.3	3.6	0.4	6.8	5.6	1.4
OSTEICHTHYES									
Unidentified fish	30.6	25.0	6.3	21.7	17.9	8.5	27.1	22.2	7.6
<u>Etrumeus teres</u>	2.8	2.3	4.9	4.3	3.6	3.1	3.4	2.8	3.9
<u>Sardinops ocellata</u>	27.8	22.7	44.8	39.1	39.3	69.0	32.2	29.2	59.1
<u>Engraulis capensis</u>	22.2	31.8	17.6	13.0	10.7	3.0	18.6	23.6	9.0
<u>Trachurus trachurus</u>	2.8	2.3	4.6	8.7	7.1	7.7	5.1	4.1	6.4
<u>Pomadasys olivaceum</u>	2.8	2.3	2.7	4.3	3.6	0.7	3.4	2.8	1.5
Sparidae	2.8	2.3	2.9				1.7	1.4	1.2
<u>Pagellus natalensis</u>	2.8	2.3	13.3	4.3	3.6	3.7	3.4	2.8	7.6
<u>Sarpa salpa</u>				4.3	3.6	1.4	1.7	1.4	0.8
<u>Spondyliosoma emarginatum</u>				4.3	3.6	1.4	1.7	1.4	0.8
Totals	36	44	482.2	23	28	698.9	59	72	1181.1

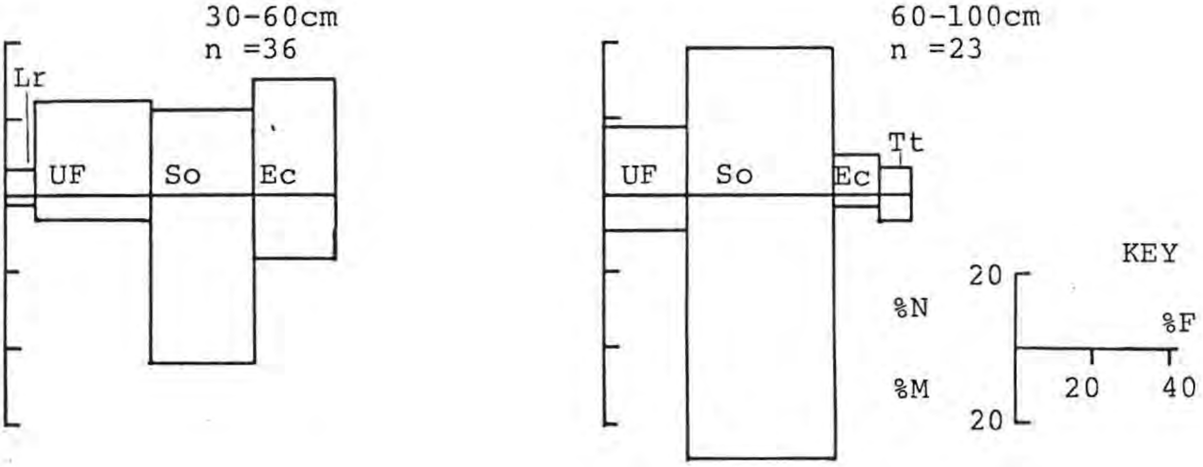


Fig. 18. Principal prey of Atractoscion aequidens.

En:Engraulis capensis Lr:Loligo reynaudi So:Sardinops ocellata
Tt:Trachurus trachurus UF:Unidentified fish

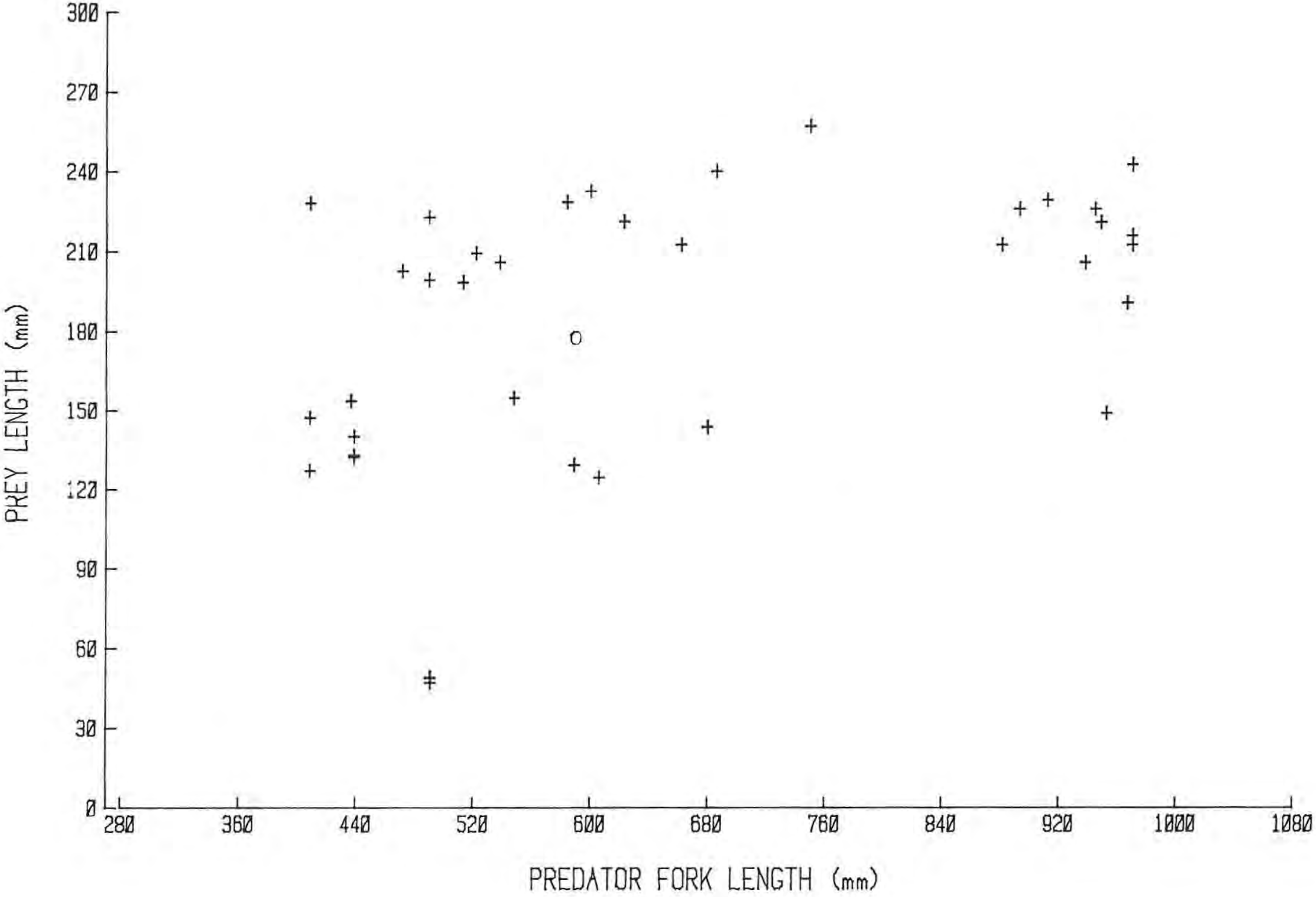


Fig. 19. Scatter diagram of prey length against fork length of *Atractoscion aequidens*. A cephalopod is shown by the circle, fishes by crosses.

Discussion

Druzhinin & Filatova (1979) record A. aequidens off the Gulf of Aden on sand and stone substrates during a trawl survey. During the current programme line fishermen caught geelbek over both reef and sandy substrates, frequently well off the bottom, indicating that it is a pelagic species. This is further suggested by the elongate silver body and the lunate tail.

Analysis of stomach contents revealed that pelagic schooling fishes, particulary S. ocellata and E. capensis are the principal components of the diet. However, demersal fish are also taken, particularly Pomadasys olivaceum and Pagellus natalensis, probably when pelagic prey are less abundant. Nepgen (1982) reported that the majority of A. aequidens in False Bay in 1980 predominantly took pelagic fish (65%F), but also noted demersal and benthic fish and octopods in the stomach contents. His results support the findings of this study.

Although the prey of the two size groups was found to be very similar (67%), they are markedly different to juveniles of 71 - 164 mm (Smale in prep.). The small trawled fish took mysids although P. olivaceum and Cynoglossus sp. were taken by geelbek larger than 143 mm.

Family: Scombridae Katsuwonus pelamis (Linnaeus, 1758)
Common name: skipjack

Description

The body is elongate and fusiform (Fig.3), moderately deep at its widest point, 25% FL (45% with dorsal and pelvic extended). The dorsal fin may be folded into a groove along the back. The second dorsal is raised and followed by 7 to 9 finlets, and the anal fin by 7 to 8 finlets. The pectoral and pelvic fins are small and may be flattened into recesses. The narrow caudal peduncle has a distinct lateral fleshy keel. The rigid caudal fin is strongly forked. The head, pointed anteriorly, is large (29% FL). The eye is big (4.5% FL). The mouth is large, the maxillary extending midway below the eye. The 53 - 63 gill rakers are long and well developed. Both jaws bear minute teeth in several rows. The body is dark blue dorsally and silvery white ventrally. Four to six dark lines occur ventrally although they are not always visible under water. Bright blue lines may be seen dorsally especially when feeding (shown in Smith 1972, plate 65). This fish rarely exceeds 75 cm in southern Africa and the South African angling record is 9.1 kg (van der Elst 1981). The largest fish on scientific record is 22 kg (Magnuson, 1973) although larger specimens are rumoured to have been caught.

Distribution and habitat

K. pelamis is an oceanic epipelagic species which is cosmopolitan in tropical and subtropical waters (Collette 1978) approximately between 56°N and 40°S, but more commonly closer to the equator (Blackburn 1965). It is usually associated with warm water of 17 - 28°C (Laevastu & Rosa 1963, in Nepgen 1970). It is found off the south-east Cape coast, becoming seasonally abundant between January and May (Talbot 1962 & pers.obs.). K. pelamis ventures inshore periodically and may be caught in Algoa Bay and other nearshore areas, normally when surface temperatures are between 18° and 25°C.

Material

A total of 765 skipjack were sampled throughout this study and 465 stomachs were collected (Fig.20). The fish were caught from widely varying localities and preliminary analysis suggested that prey taken from each of three areas was distinctly different. The three areas were defined as:

1. Inshore: coastal areas, predominantly in the whole of Algoa Bay, but also Mossel Bay within about 8 km of the coast.
2. Offshore: south of Cape Recife. The area fished is usually between 8 and 40 km south in suitably warm water, near the edge or in the Agulhas Current. The fishermen usually troll close to the lateral thermocline characteristic of the edge of the continental shelf south of Port Elizabeth.
3. East London area: fishermen here fish both close to the shore and offshore. The vagaries of the Agulhas Current, however, cause its influence to be felt close inshore. It was therefore not feasible to subdivide the sample according to distance offshore. The

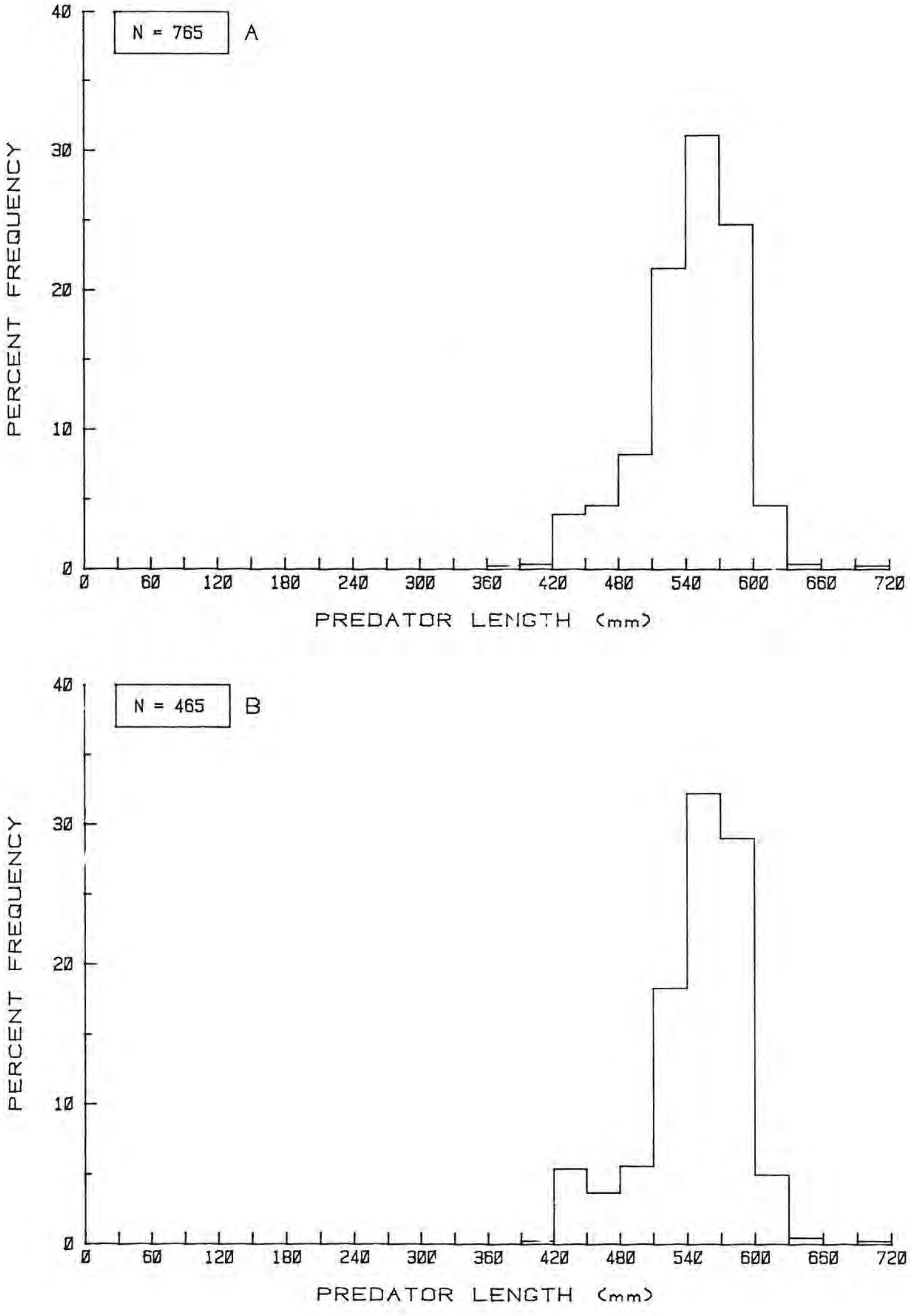


Fig. 20. Histograms of the total sample (A) of Katsuwonus pelamis and those with stomach contents (B).

proximity of the warm current to shore allows anglers to fish both areas on a particular fishing outing.

Feeding

The effect of predator size on prey selection was investigated at each of the localities.

Inshore areas provided little information (Table 11, Fig. 21) as only two size groups, 501 - 600 and 601 - 700 mm were caught there. The 501 - 600 mm group took crustaceans (72%N and 4%M), cephalopods (1%N, 3%M) and fish (28%N, 93%M). Megalopa larvae were numerically the most dominant prey (71%) and S. ocellata dominated by mass (75%M). The large size-group took only fish, although only a small sample was collected (5). S. ocellata dominated by number and mass (95% and 99% respectively). The diet of these two groups was 75% similar by prey mass.

Samples collected offshore were grouped by size: 400 - 500 mm; 501 - 600 mm and 601 - 700 mm. The small group took crustaceans (98%N, 16%M), pteropods (0.1%N, <0.1%M), cephalopods (1%N, 81%M) and fish (1%N, 4%M) Euphausids dominated by number (97%) and Lycoteuthis diadema by mass (46%). The medium- sized group took crustaceans (99%N, 10%M), pteropoda (<0.1%N, 0.1%M), cephalopods (0.3%N, 21%M) and fish (1%N, 70%M). Euphausids dominated by number (98%) and E. teres by mass (39%). The large group took crustaceans (71%N, 5%M), cephalopods (8%N, 13%M) and fish (21%N, 82%M). Megalopa larvae dominated by number (61%N) and E. teres and S. ocellata by mass (38% and 37%). The two most similar groups were the larger two (63%) and the 400 - 500 mm group was 21% similar to them (Fig. 22).

The East London material was grouped into the same 3 size groups. The small group took crustaceans (33%N, 4%M), pteropods (28%N, 1%M), cephalopods (15%N, 63%M) and fish (25%N, 33%M). Megalopa larvae and pteropods dominated by number (31% and 28%) and ommastrephids dominated by mass (35%). The 501 - 600 mm group took crustaceans (18%N, 2%M), unidentified molluscs and pteropods (25%N, 1%M), cephalopods (17%N, 65%M) and fish (41%N, 33%M). Pteropods dominated numerically (25%) and ommastrephid squids dominated by mass (59%). The 601 - 700 mm group took crustaceans (25%N, 1%M), cephalopods (26%N, 77%M) and fish (49%N, 23%M).

Table 11 (a). The prey of Katsuwonus pelamis taken inshore, according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	501 - 600 mm %F	%N	%M	601 - 700 mm %F	%N	%M
CRUSTACEA						
Unidentified crustaceans	3.0	1.0	0.2			
Megalopa larvae	19.4	70.7	3.9			
MOLLUSCA						
Teuthoidea	3.0	0.2	0.8			
Loligo reynaudi	6.0	0.5	2.0			
OSTEICHTHYES						
Unidentified fish	6.0	0.5	1.2	20.0	5.0	0.8
Etrumeus teres	13.4	1.6	4.5			
Sardinops ocellata	53.7	16.9	74.5	80.0	95.0	99.2
Engraulidae	1.5	0.2	0.1			
Engraulis capensis	32.8	7.4	10.7			
Scomberesox saurus	4.5	0.6	1.8			
Petalichthys capensis	1.5	0.1	0.4			
Scomber japonicus	1.5	0.1	<0.1			
Stromateidae	1.5	0.1	<0.1			
Totals	67	813	3834.4	5	20	393

Table 11 (b). The prey of *Katsuwonus pelamis* taken 8 - 40 km south of Cape Recife, according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	400 - 500 mm %F	%N	%M	501 - 600 mm %F	%N	%M	601 - 700 mm %F	%N	%M
CRUSTACEA									
Unidentified crustaceans				0.4	0.1	<0.1			
Isopoda				0.4	<0.1	<0.1			
Stomatopoda	2.8	<0.1	0.1	11.8	0.1	0.3	25.0	9.8	1.2
Euphausiacea	19.4	97.3	14.9	15.0	97.8	8.4			
Megalopa larvae	36.1	0.8	0.6	34.2	1.0	1.0	62.5	60.7	3.3
Pteropoda	2.8	0.1	<0.1	5.1	0.1	0.1			
MOLLUSCA									
Sepiidae				0.4	<0.1	0.1	12.5	1.6	0.2
Teuthoidea	25.0	0.4	20.1	3.5	<0.1	0.9	25.0	3.3	12.0
Loligo reynaudi				2.4	<0.1	3.3	12.5	3.3	1.2
Lycoteuthis diadema	27.8	0.5	46.1	13.8	0.2	14.7			
Ommastrephidae	25.0	0.3	14.3	2.4	<0.1	1.5			
Ocythoe sp.				0.4	<0.1	<0.1			
OSTEICHTHYES									
Unidentified fish	25.0	0.4	2.0	9.1	0.1	1.7	12.5	1.6	4.1
Etrumeus teres				28.3	0.3	39.4	37.5	4.9	38.0
Sardinops ocellata				8.7	0.1	16.7	37.5	11.5	36.7
Engraulis capensis				3.2	0.1	2.5			
Myctophidae				0.4	<0.1	<0.1			
Diaphus sp.	5.6	0.1	0.1						
Exocoetidae				1.2	<0.1	0.6			
Oxyporhamphus sp.				0.4	<0.1	1.6			
Scomberesox saurus				4.7	0.1	5.8	12.5	1.6	2.9
Apogonidae	8.3	0.1	0.5	0.4	<0.1	<0.1			
Carangidae				0.8	<0.1	0.4			
Scomber japonicus				1.2	<0.1	1.0			
Cubiceps sp.	2.8	<0.1	0.4						
Stomateidae	5.6	0.1	0.1	3.5	<0.1	<0.1	12.5	1.6	0.4
Balistidae	2.8	<0.1	0.2	0.8	<0.1	0.1			
Laputa sp.	2.8	<0.1	0.4						
Totals	36	3465	460.4	254	36601	8106	8	61	242

Table 11 (c). The prey of *Katsuwonus pelamis* taken off East London, according to size. The totals are number of stomach (F), number of items (N) and prey wet mass (M), g.

Prey	401 - 500 mm			501 - 600 mm			601 - 700 mm		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA									
Copepoda				1.4	0.4	0.1			
Stomatopoda	11.8	2.1	0.8	15.9	9.2	1.0	22.2	4.3	0.1
Penaeidea							11.1	1.4	0.2
Megalopa larvae	47.1	30.9	2.7	26.1	8.8	0.5	22.2	18.8	0.3
MOLLUSCA									
Unidentified molluscs				1.4	0.2	0.1			
Pteropoda	23.5	27.7	1.3	13.0	24.5	1.3			
Sepiidae				1.4	0.4	1.9			
Teuthoidea				2.9	0.4	0.6			
Lycoteuthis diadema	5.9	3.2	21.6	4.3	0.7	2.7			
Abraliopsis sp.				2.9	0.4	0.4			
Ommastrephidae	23.5	10.6	34.8	29.0	13.8	59.0	44.4	26.1	76.7
Thysanoteuthis sp.				1.4	0.2	0.3			
Octopoda (Pelagic)				1.4	0.5	0.1			
Ocythoe sp.				1.4	0.2	<0.1			
Argonauta spp.	5.9	1.1	6.3	1.4	0.2	0.1			
OSTEICHTHYES									
Unidentified fish	41.2	14.9	15.7	26.1	7.2	3.4	22.2	2.9	0.4
Etrumeus teres				10.1	1.8	7.9	22.2	5.8	11.4
Sardinops ocellata	5.9	1.1	14.6	2.9	0.4	2.3			
Engraulis capensis				17.4	5.0	9.5			
Myctophidae				2.9	10.6	1.8			
Exocoetidae	5.9	2.1	0.5	2.9	0.4	0.2	11.1	1.4	0.3
Scomberesox saurus				1.4	0.2	0.6			
Cheilodactylidae				2.9	7.6	3.3	11.1	37.7	10.5
Priacanthidae				1.4	0.2	<0.1			
Priacanthus sp.				1.4	1.3	0.5			
Apogonidae							11.1	1.4	0.2
Carangidae				5.8	0.7	0.2			
Trachurus trachurus				1.4	0.2	0.8			
Scomber japonicus				1.4	0.2	0.5			
Nomeidae				1.4	0.2	0.1			
Stromateidae	5.9	3.2	0.3	4.3	0.9	0.2			
Bramidae				1.4	0.9	0.4			
Sphyraenidae	5.9	1.1	0.2						
Balistidae				4.3	0.5	0.3			
Laputa sp.	5.9	2.1	1.3	4.3	2.2	0.5			
Totals	17	94	157.7	69	556	1554.1	9	69	665.2

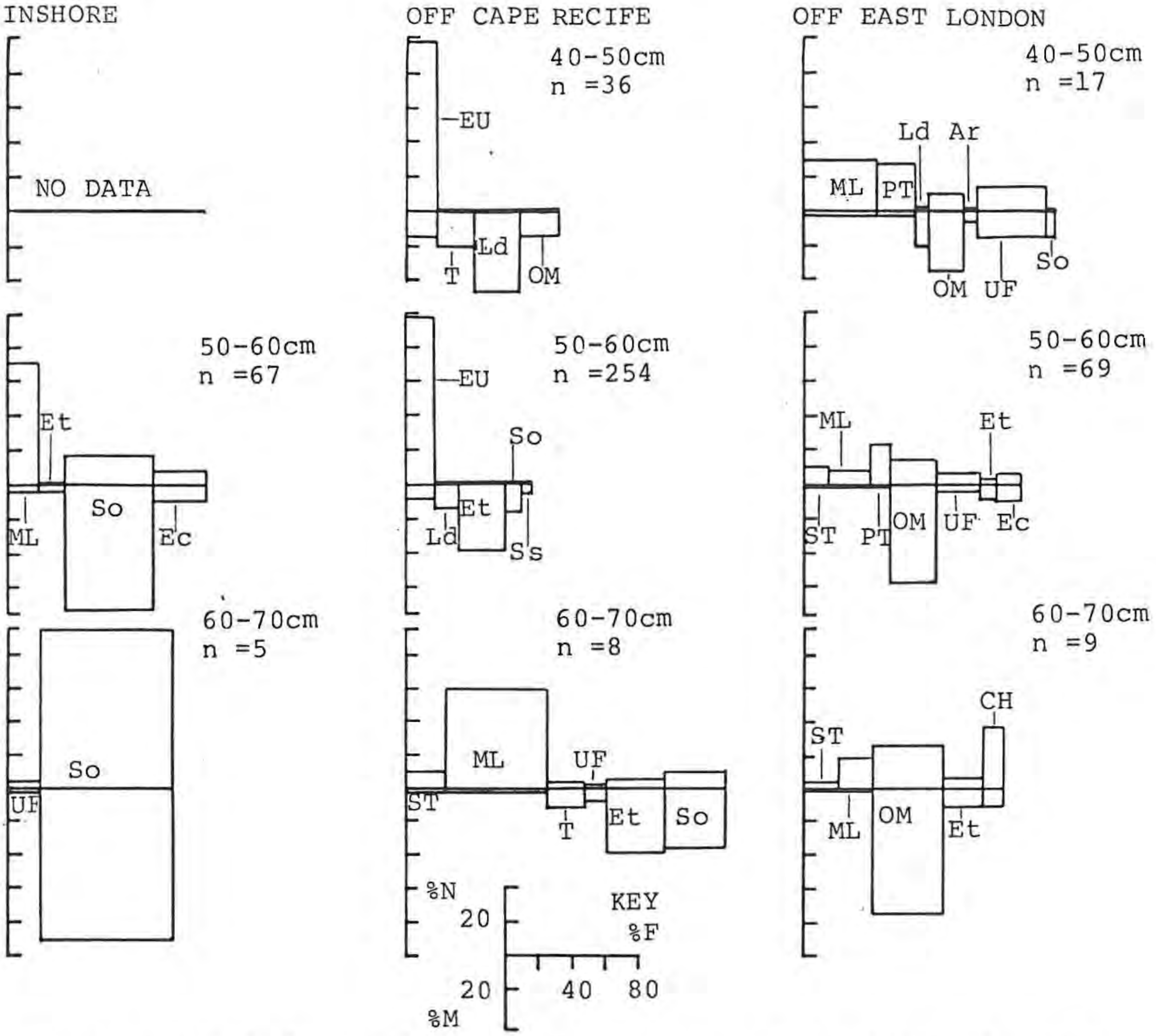


Fig. 21. Principal prey of Katsowonus pelamis taken inshore (0-8 km), off Cape Recife (8-40 km) and off East London by different size fish.

Ar:Argonauta spp. CH:Cheilodactylidae Ec:Engraulis capensis Et:Etrumeus teres EU:Euphausiacea Ld:Lycoteuthis deadema ML:Megalopa larvae OM:Ommastrephidae PT:Pteropod So:Sardinops ocellata Ss:Scomberesox saurus ST:Stomatopoda T:Teuthoidea UF:Unidentified fish.

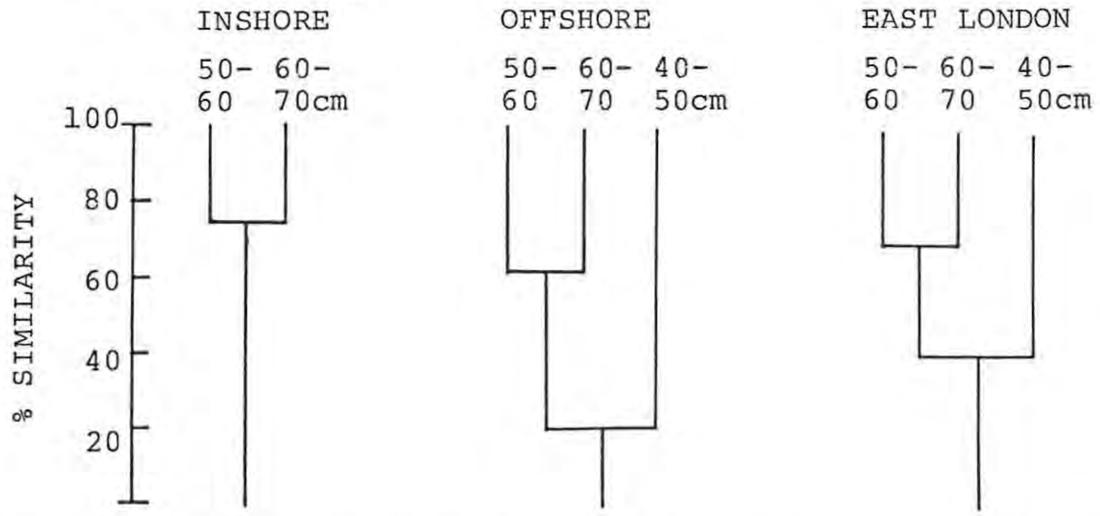


Fig. 22. Similarity diagrams of diets of Katsuwonus pelamis size groups, according to prey mass. Each was calculated separately according to locality.

Cheilodactylid larvae dominated by number (38%) and ommastrephid squid dominated by mass (77%). Off East London cephalopods were dominated by Lycoteuthis diadema and the Ommastrephidae. It is noteworthy that these two groups reverse their importance here compared with offshore of Cape Recife. Unidentified juvenile fishes, Etrumeus teres and Cheilodactylidae early juveniles were important sporadically and probably reflect a patchy distribution of prey. The 501 - 600 and 601 - 700 mm groups were most similar (71%) and the 401 - 501 group was 41% similar to this pair by prey mass (Fig. 22).

Predator-prey length relationship

The size of prey taken by K. pelamis is plotted in Fig.23. A wide range of prey were taken by K. pelamis and the ratio of prey length to predator length varied from 0.2 - 79%. Small crustaceans and some oceanic cephalopods are not included as no regression data were available and measurements of the small crustaceans were not taken. The relationship for the four principal teleosts taken were: Engraulidae 11 - 28%; Sardinops ocellata 20 - 54%; E. teres 13 - 43% and Scomberesox saurus 37 - 79%.

It appears that prey size selection is strongly influenced by prey availability. Considering the large number of crustaceans taken, such as euphausids and crab megalopae, the lower limit would commonly be less than 1% of predator length. In the case of euphausids these prey are probably taken 'en masse' from a swarm while megalopa larvae may be taken individually.

Important fish prey common to the different size groups are plotted in Fig.24. Those shown are Sardinops ocellata, E. teres and Scomberesox saurus. There is considerable overlap in the size of fishes taken and no trend in size selection is evident.

Seasonality of prey selected.

Prey selectivity was examined according to bimonthly intervals at each locality. Material was not separated into size groups as there were insufficient data for most months. Material was available from inshore areas only from January to April (Table 12). S. ocellata and E. capensis

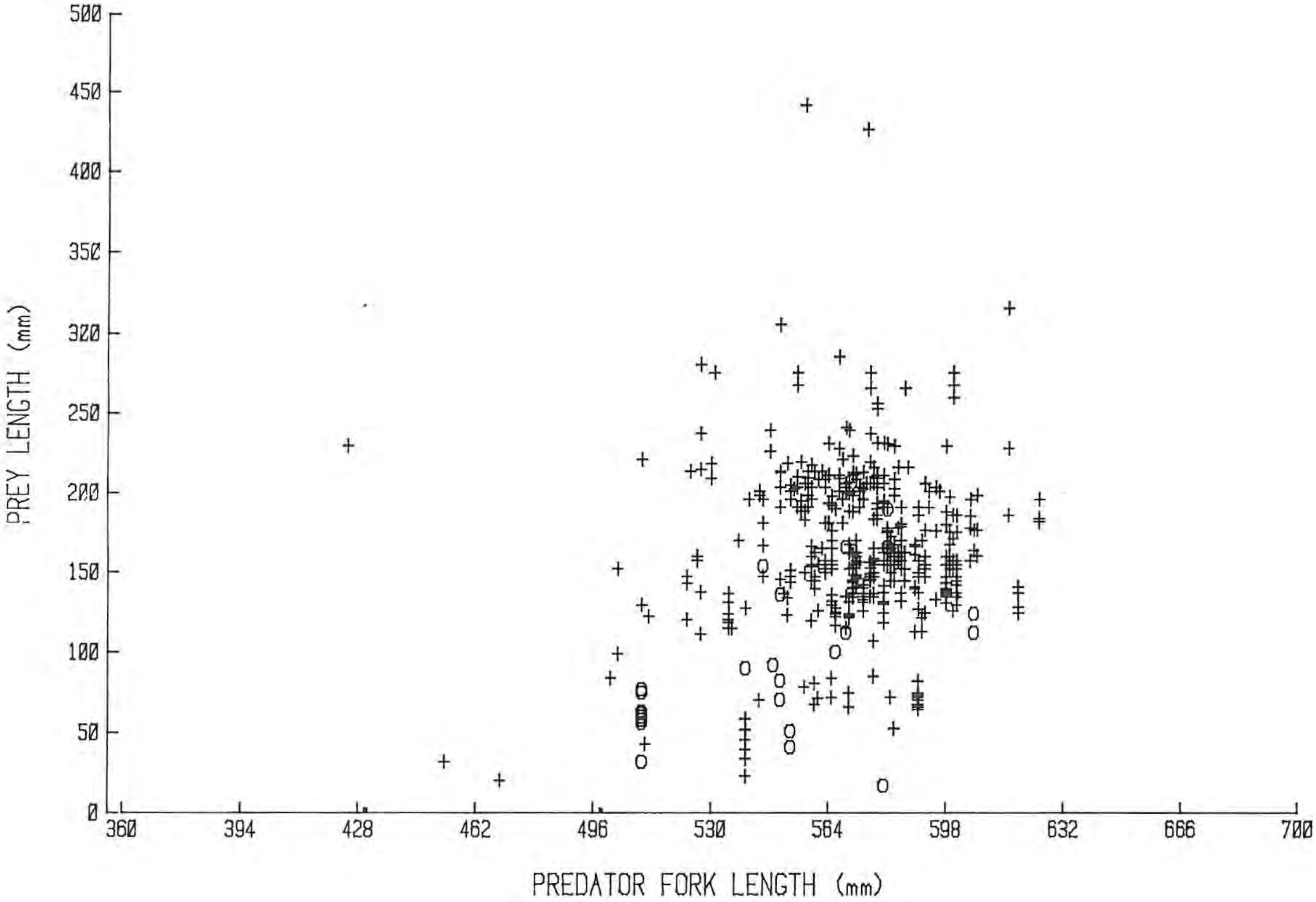


Fig. 23. Scatter diagram of prey length against fork length of _Katsuwonus pelamis_. Crustaceans are shown by dots, cephalopods by circles and fishes by crosses.

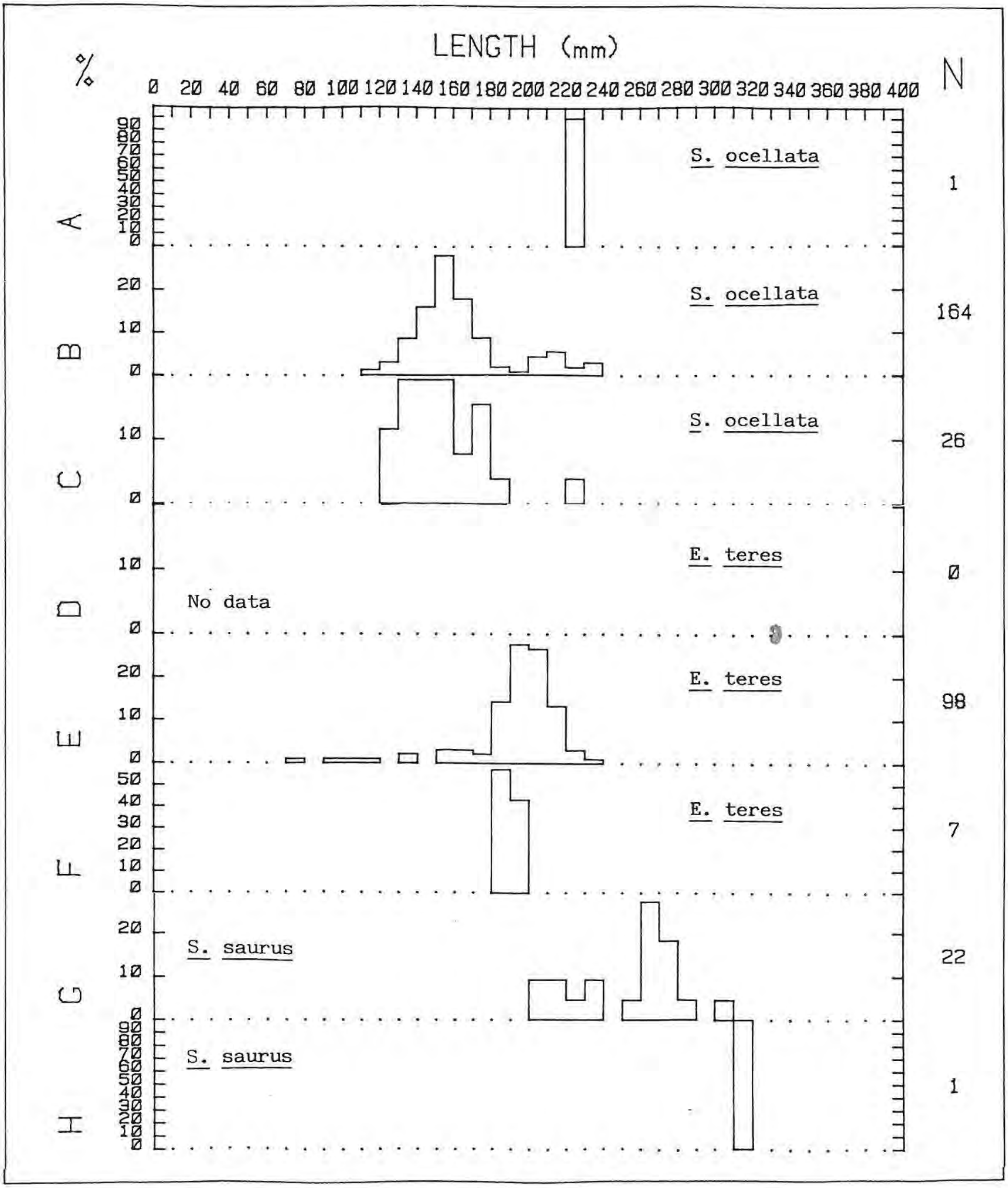


Fig. 24. Histograms of common prey of Katsuwonus pelamis of 401 - 500 mm (A,D), 501 - 600 mm (B,E,G) and 601 - 700 mm (C,F,H). Sardinops ocellata (A,B,C); Etrumeus teres (D,E,F) and Scomberesox saurus (G,H) are shown. Two fish larger than 400 mm are not shown in G.

Table 12 (a). The prey of *Katsuwonus pelamis* taken inshore in bi-monthly periods, all years combined. Totals are number of stomachs (F), number of items(N) and prey wet mass (M), g.

Prey	January-February			March-April		
	%F	%N	%M	%F	%N	%M
CRUSTACEA Unidentified crustaceans				2.9	1.0	0.2
Megalopa larvae				18.8	70.8	3.8
MOLLUSCA						
Teuthoidea				2.9	0.2	0.8
Loligo reynaudi				5.8	0.5	2.0
OSTEICHTHYES				7.2	0.6	1.2
Etrumeus teres				13.0	1.6	4.4
Sardinops ocellata	33.3	33.3	57.5	56.5	18.4	78.6
Engraulidae				1.4	0.2	0.1
Engraulis capensis	66.7	57.1	40.8	29.0	5.9	6.8
Scomberesox saurus	33.3	4.8	1.7	2.9	0.5	1.6
Petalichthys capensis				1.4	0.1	0.4
Scomber japonicus	33.3	4.8	0.1			
Stromateidae				1.4	0.1	<0.1
Totals	3	21	360	69	812	3867.4

Table 12 (b). The prey of *Katsuwonus pelamis* taken 8 - 40 km south of Cape Recife in bi-monthly periods, all years combined. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	January-February			March-April			May-June			November-December		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Unidentified crustaceans				0.4	<0.1	<0.1						
Isopoda				0.4	<0.1	<0.1						
Stomatopoda	8.0	2.4	0.1	13.3	0.2	0.3				25	0.1	1.5
Euphausiacea				16.4	98.1	9.3	14.0	93.8	8.0	50	99.6	95.4
Megalopa larvae	44.0	55.4	0.6	32.7	0.8	0.8	44.2	3.4	3.3	25	0.2	2.3
MOLLASCA												
Ptetropoda	8.0	2.4	<0.1	4.9	0.1	0.1	2.3	0.1	<0.1			
Sepiidae				0.9	<0.1	0.1						
Teuthoidea				4.4	<0.1	1.4	23.3	0.5	13.5			
Loligo reynaudi				3.1	<0.1	3.8						
Lycoteuthis diadema	16.0	9.6	24.3	12.4	0.1	10.9	30.2	0.8	57.4			
Ommastrephidae				1.8	<0.1	1.3	25.6	0.5	13.7			
Ocythoe sp.	4.0	1.2	0.1									
OSTEICHTHYES												
Unidentified fish				9.7	0.1	1.9	23.3	0.6	2.2	25	0.1	0.8
Etrumeus teres	40.0	19.3	55.2	28.8	0.2	38.8						
Sardinops ocellata	8.0	2.4	7.0	10.2	0.1	19.2						
Engraulis capensis	4.0	2.4	2.0	2.7	0.1	2.6	2.3	<0.1	0.4			
Myctophidae							2.3	<0.1	0.1			
Diaphus sp.							4.7	0.1	<0.1			
Exocoetidae				1.3	<0.1	0.7						
Oxyporhamphus sp.				0.4	<0.1	1.8						
Scomberesox saurus	4.0	3.6	10.8	5.3	0.1	5.3						
Apogonidae				0.4	<0.1	0.1	7.0	0.1	0.3			
Carangidae				0.9	<0.1	0.5						
Scomber japonicus				1.3	<0.1	1.1						
Cubiceps sp.							2.3	<0.1	0.3			
Stromateidae	4.0	1.2	<0.1	4.0	<0.1	<0.1	4.7	0.1	0.1			
Balistidae				0.9	<0.1	0.1	2.3	<0.1	0.1			
Laputa sp.							2.3	<0.1	0.3			
Totals	25	83	904.5	226	35814	7185.6	43	2972	692.3	4	1258	25.9

Table 12 (c). The prey of *Katsuwonus pelamis* taken off East London in bi-monthly periods, all years combined. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	January-February			March-April			May-June			July-August			September-October			November-December		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA																		
Copepoda				2.2	0.6	<0.1												
Stomatopoda	18.2	14.0	0.7	20.0	12.3	0.9	15.0	2.6	0.3	16.7	7.1	1.0						
Panaeidea				2.2	0.3	0.1												
Megalopa larvae	9.1	8.8	0.2	35.6	12.5	0.4	45.0	23.2	1.5	16.7	7.1	1.3				8.3	4.1	0.5
MOLLUSCA																		
Unidentified molluscs	9.1	1.8	0.7															
Pteropoda	18.2	14.0	0.2	13.3	22.5	1.1	20.0	47.7	0.9	16.7	21.4	2.1						
Sepiidae				2.2	0.6	1.8												
Teuthoidea	9.1	1.8	<0.1	2.2	0.3	0.6												
Lycoteuthis diadema	18.2	3.5	10.6				10.0	3.3	17.4									
Abraliopsis sp.				4.4	0.6	0.4												
Ommastrephidae				51.1	27.6	86.1	20.0	4.6	19.4							8.3	0.7	2.3
Thysanoteuthis sp.				2.2	0.3	0.2												
Octopoda (Pelagic)				2.2	0.9	0.1												
Ocythoe sp.,																8.3	0.7	0.2
Argonauta spp.				4.4	0.6	0.7												
OSTEICHTHYES																		
Unidentified fish	36.4	8.8	17.3	26.7	8.8	1.4	30.0	6.6	4.2	50.0	57.1	36.2				16.7	1.4	2.0
Etrumeus teres	9.1	1.8	4.9	8.9	1.4	1.9	20.0	5.3	46.0									
Sardinops ocellata				2.2	0.3	0.3	5.0	0.7	8.6	16.7	7.1	59.4						
Engraulis capensis	36.4	19.3	55.8	6.7	2.3	1.8										41.7	6.2	19.7
Myctophidae	9.1	1.8	0.4													8.3	40.0	14.1
Exocoetidae				6.7	0.9	0.3	5.0	1.3	0.2									
Scomberesox saurus				2.2	0.3	0.6												
Cheilodactylidae																25.0	46.9	61.1
Priacanthidae				2.2	0.3	<0.1												
Priacanthus sp.	9.1	12.3	4.9															
Apogonidae							5.0	0.7	0.3									
Carangidae	9.1	1.8	0.7	6.7	0.9	0.1												
Trachurus trachurus													100	100	100			
Scomber japonicus				2.2	0.3	0.4												
Nomeidae				2.2	0.3	0.1												
Stromateidae	18.2	5.3	2.1	2.2	0.6	<0.1	5.0	2.0	0.1									
Bramidae				2.2	1.4	0.4												
Sphyraenidae							5.0	0.7	0.1									
Balistidae				2.2	0.3	<0.1	10.0	1.3	1.0									
Laputa sp.	9.1	5.3	1.4	6.7	3.1	0.5												
Totals	11	57	142.1	45	351	1636.2	20	151	350	6	14	38.7	1	1	12	12	145	198

dominate by number and mass in January (33%N, and 58%M, 57%N and 41%M, respectively). In March-April megalopa larvae dominated by number (71%) but S. ocellata dominated by mass (79%).

Offshore material was available for January-June and November-December, the bulk being collected in March-April (226 stomachs). The importance of different groups varies, but euphausids, Lycoteuthis diadema and Etrumeus teres appear to be the more dominant prey.

Off East London material was collected in each bi-monthly period. Megalopa larvae and Stomatopoda were recorded in most periods while cephalopods and fish varied in importance. The dominance of ommastrephid squids in March-April is noteworthy while E. capensis dominates at both the beginning and end of the year. S. ocellata is more important in the middle of the year. Cheilodactylid larvae were dominant by number and mass in November-December (47%N, 61%M).

Annual variation

The annual variation in prey taken in Algoa Bay and environs is presented in Table 13 for 1978 and 1980. No data were collected in 1979. The principal prey species in 1978 was S. ocellata, which contributed 85% of prey mass and occurred in 65% of the stomachs examined. Megalopa larvae were numerically dominant (73%N). In 1980 S. ocellata was less important, contributing 44% of prey mass while E. capensis made up 38% of the mass. E. capensis was taken frequently (67%F) and was numerically important (58.8%N).

Stomach fullness indices.

The mean stomach fullness index was 0.9% of body mass (n=403). The highest value recorded was 7.9%. The mean "consumption index" was 1.5% (n=391) and the highest recorded value was 7.2%.

Feeding observations

On one occasion K. pelamis were observed feeding on a bunched school of Sardinops ocellata between Riybank and St Croix, Algoa Bay, on March 14, 1978. Gannets, Sula capensis (Lichtenstein, 1823), and penguins, Spheniscus demersus (Linnaeus, 1758) were also attacking the school close to the water surface. Snorkel diving observations were made as the

Table 13. The prey of *Katsuwonus pelamis* taken in Algoa Bay and environs in different years of the study. The totals are numbers of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	1978 %F	%N	%M	1980 %F	%N	%M
CRUSTACEA	3.3	1.0	0.2			
Megalopa larvae	21.7	73.4	4.1			
Teuthoidea	3.3	0.3	0.9			
Loligo reynaudi	3.3	0.3	1.1			
OSTEICHTHYES						
Unidentified fish	8.3	0.6	1.3			
Etrumeus teres	15.0	1.7	4.8			
Sardinops ocellata	65.0	19.0	84.7	11.1	20.6	43.9
Engraulidae	1.7	0.3	0.1			
Engraulis capensis	21.7	3.3	2.8	66.7	58.8	38.4
Scomberesox saurus				33.3	14.7	14.6
Petalichthys capensis				11.1	2.9	3.1
Scomber japonicus				11.1	2.9	<0.1
Stromateidae	1.7	0.1	<0.1			
Totals	60	783	3587.4	9	34	472

school swam close to the boat. The prey formed a tight, circling ball which the gannets attacked by plunge feeding and stabbing from the surface. Several penguins (3-5) were underwater and swam rapidly through the school, circling below them, thereby preventing their descent between forays. The skipjack were swimming at extremely high speeds and were recognisable mainly by the irridescent blue marks on their flanks. They were out of sight most of the time, but occasionally darted through the school. The speed at which the skipjack travelled clearly indicated they would be able to out-swim prey and would probably surprise the schooling prey.

During this frenzy three sharks (including Carcharhinus brachyurus (Günther 1870) of 1.2 m TL) were also seen attacking the school of S. ocellata.

Discussion

Skipjack tuna are distributed widely, between approximately 56°N and 40°S. Williams (1962) reported that K. pelamis occurs off East Africa between 1°30'S and 10°30'E, mainly inside the 100 fm line. Talbot (1962) recorded skipjack on the south and east coasts of South Africa, occasionally abundant in summer west of the Cape Peninsula. The present study revealed that K. pelamis occurs sporadically in large numbers in inshore waters such as Algoa Bay. In March and April 1978 it was particularly abundant in the Bay, but was not caught there in 1979, and was caught infrequently in 1980. Offshore, in close proximity to the Agulhas Current, skipjack may occur throughout the year, but appear to be particularly abundant in March to May. In this study it was not possible to quantify these observations because poor weather prevented ski-boat fishermen from fishing offshore every month. It is possible that inshore waters are not suitable for skipjack throughout the year.

Temperature appears to play a large part in determining the limits of many species of tuna (Blackburn 1965) although Blackburn (1969) found that they will occasionally enter water of 17°C, but not lower, appearing to prefer waters of 20°C and above. In a more recent review, Matsumoto & Skillman (cited in Barkley et al. 1978) found that the sea surface temperature for fisheries of skipjack in total varies from 15° to 30°C. More precise physiological experiments have revealed that the habitat of the skipjack is defined by oxygen and temperature profiles (Neil et al. 1976, Dizon et al. 1977). Barkley et al. (1978) found that the habitat is restricted with lower limits of about 18°C, while the upper limit varies from 30°C for small specimens to about 20°C for larger individuals. High dissolved oxygen concentrations of at least 4 -5 ppm were necessary. They suggest that because of elevated temperatures and the difficulty dumping excess heat during rigorous activity, only smallest individuals can inhabit warm surface waters of the tropics while those larger than 4 - 5 kg must inhabit the thermocline. This suggests that habitat partitioning occurs and may partly explain differences in prey taken offshore by small and large skipjack.

Experiments in the wild, in which free ranging tuna were equipped with ultrasonic tags, have revealed that small fish are associated with banks during the day but that they move away at night (Yuen 1970). Dizon et al. (1978) found that the three fish of about 700 mm which they had tagged spent 85% of the tracking time in water above 20°C, but ventured occasionally into cold water which could have been lethal for indefinite exposures, 12° - 14°C being the lowest recorded. As no thermocline was present during that experiment, its influence on the behaviour of the fish could not be measured. However, the activity-size boundaries hypothesized by Neil et al. (1976) were not violated in this study. The smaller fish behaved in a similar manner to those studied by Yuen (1970).

Another factor which may govern distribution of K. pelamis is water transparency as tuna are believed to locate their prey visually at close range (Magnuson 1963). Limited data are available although secchi values of 15 - 35 m have been given (Blackburn 1965) for good tuna fishing. Salinity has also been considered important, although Dizon et al. (1978) found that small variations in salinity (to 20‰) had no measurable effect on the swimming speed of captive fish and considered that small changes were not important behavioural regulators.

These factors would also affect the distribution of K. pelamis in the study area and may account for their absence inshore during much of the year. No measurements of any of the relevant parameters were made, owing to the opportunistic sampling from ski-boats.

The streamlined body, strongly lunate tail with a narrow caudal peduncle and body temperatures raised above environmental temperatures all indicate the extremely specialised nature of this predator. K. pelamis is clearly well equipped to outswim prey and escape predation itself. Speeds of up to 950 cm/sec have been noted during burst swimming, and yellowfin tuna appear to attain about the same or greater speeds (Magnuson 1978). As K. pelamis inhabits the water column, it is clear why this species took schooling squids and fishes.

Similar variations in prey taken from different areas and by different sizes of skipjack have been shown by several authors (Yuen 1959, Waldron & King 1963, Dragovich 1971, Dragovich & Pothoff 1972). Magnuson & Heitz (1971) have shown that the small prey taken by young K. pelamis and the frequent occurrence of crustaceans in the diet results from the efficiency of the many elongate gill rakers which are characteristic of this species. Of eight scombrid and two coryphaenid species, K. pelamis was a species particularly well adapted for filtering euphausids. These authors suggest that the selective feeding which occurs between scombrids and coryphaenids is often masked by the diverse fauna taken. Their findings were confirmed in this study. It appears that selective feeding becomes important in areas where food is more limited and patchy, such as offshore areas compared to coastal areas where schooling pelagic teleosts are abundant. Intraspecifically there is greater overlap in prey species and size taken inshore than offshore. This again results from both size groups taking abundant schooling coastal fishes inshore. In addition to the differences described between inshore and offshore areas, a further difference was recorded off East London where a greater variety of prey was noted. This probably results from the more diverse sub-tropical fauna there.

Examination of original stomach contents and the reconstructed masses revealed that the highest original mass was about 8% of body mass while the reconstructed mass was 7%. These figures correspond well with other studies on feeding. Magnuson (1969) has reported on experiments on food consumption and digestion by K. pelamis in captivity. He showed that fish ate about 8.6% of the body weight and that about 10% of the original weight eaten passed from the stomach each hour. Fifty per cent had been passed after 5 hours and the stomach was emptied in 12 hours. Such gastric evacuation rates are faster than those of equivalent sized fish of other species. The difference was not entirely attributable to the elevated body temperature of the skipjack (Magnuson 1969). Repeated feeding of experimental fish through the day indicated that the maximum capacity of the stomach was about 7% but a total equivalent to 15% of the body mass was taken in a day. The reconstructed stomach mass recorded in this study confirms that gastric evacuation is rapid and that there is no retention of hard parts in the stomach.

The mean percentage stomach mass (0.9%) was considerably lower than the maximum values. Raju (1964) recorded a maximum of 6.3% and a mean of 1.5%, although these included bait. In the central Pacific, means of 0.8% (Waldron & King 1963, reported in Magnuson 1969) and 1.0% for natural food have been recorded (Yuen 1959). Dragovich (1971) found that 99% of the stomachs examined were below the 7% possible maximum in his study of Atlantic ocean skipjack. The results conform with findings made in the present study.

The difference between maximum stomach content weight and the average weight found in skipjack stomachs suggests that skipjack feed repeatedly throughout the day and that this is necessitated by the patchy distribituion of the prey. Magnuson (1969) pointed out that although skipjack often have an early morning peak of feeding, they frequently feed through the day in sporadic peaks of activity. Rapid digestion allows the skipjack to take on the next abundant prey patch although it also illustrates the high metabolic cost of continuous swimming and elevated body temperatures in this species.

Family: Scombridae Thunnus albacares (Lowe, 1839)
Common name: yellowfin tuna

Description

The body is fusiform, elongate and slightly compressed laterally (Fig.3). The body is moderately deep, approximately 26% FL but 40% with the dorsal and pelvic fins raised. The first dorsal fin with 13 - 14 spines is retractable into a groove. The second dorsal occurs immediately behind the first and is composed of 12 rays and 8 - 10 finlets.

The anal fin has 12 rays and 7 - 8 finlets. The dorsal and anal fins become very long in large specimens, over 20% FL. The pectoral fin is elongate although the pelvics are short and may be retracted into a groove. The lateral line runs from the operculum to the caudal peduncle in the upper third of the body in a gently curving line. The caudal peduncle is very narrow with one strong keel between two smaller keels. The rigid caudal fin is strongly forked.

The head is pointed anteriorly and large, about 29% of fork length. The eye is big (3.2 - 6.2% FL) and the large mouth is terminal. The maxilla extends to just below the eye. The gill rakers are strong and elongate. A single row of conical teeth occurs in each jaw. Colour is dark blue dorsally, becoming yellow laterally and pearly ventrally. Several lines run across the ventral area. The dorsal and anal fins are dark but tinged with yellow and the finlets are yellow. Although it attains more than 176 kg, the South African angling record is 83.9 kg (van der Elst 1981).

Distribution and habitat

T. albacares occurs from about 40°N to 35°S in all the major oceans of the world. They are epipelagic, from about 0-150 m (Blackburn 1965). They occur off the South African east coast and off the Cape mainly in summer (Talbot 1962, Suda 1973).

Material

A total of 694 Thunnus albacares of 452-1390 mm were examined. Stomach contents were collected from 614 fish of 452 - 1390 mm (Fig. 25). The high proportion of fish with stomach contents (88%) is partly attributable to the fishing method, surface trolling.

Feeding

Prey species selection by each of three size groups of tuna is presented in Table 14. The principal components are described in Fig. 26. In inshore areas 193 stomachs of fish between 400 - 600 mm FL contained 23 prey categories. Crab megalopa larvae were the most dominant invertebrates taken, accounting for 54% by number and 2% of prey mass. Etrumeus teres, Sardinops ocellata and Engraulis capensis were the three principal fish species taken. Of these, S. ocellata was dominant by mass

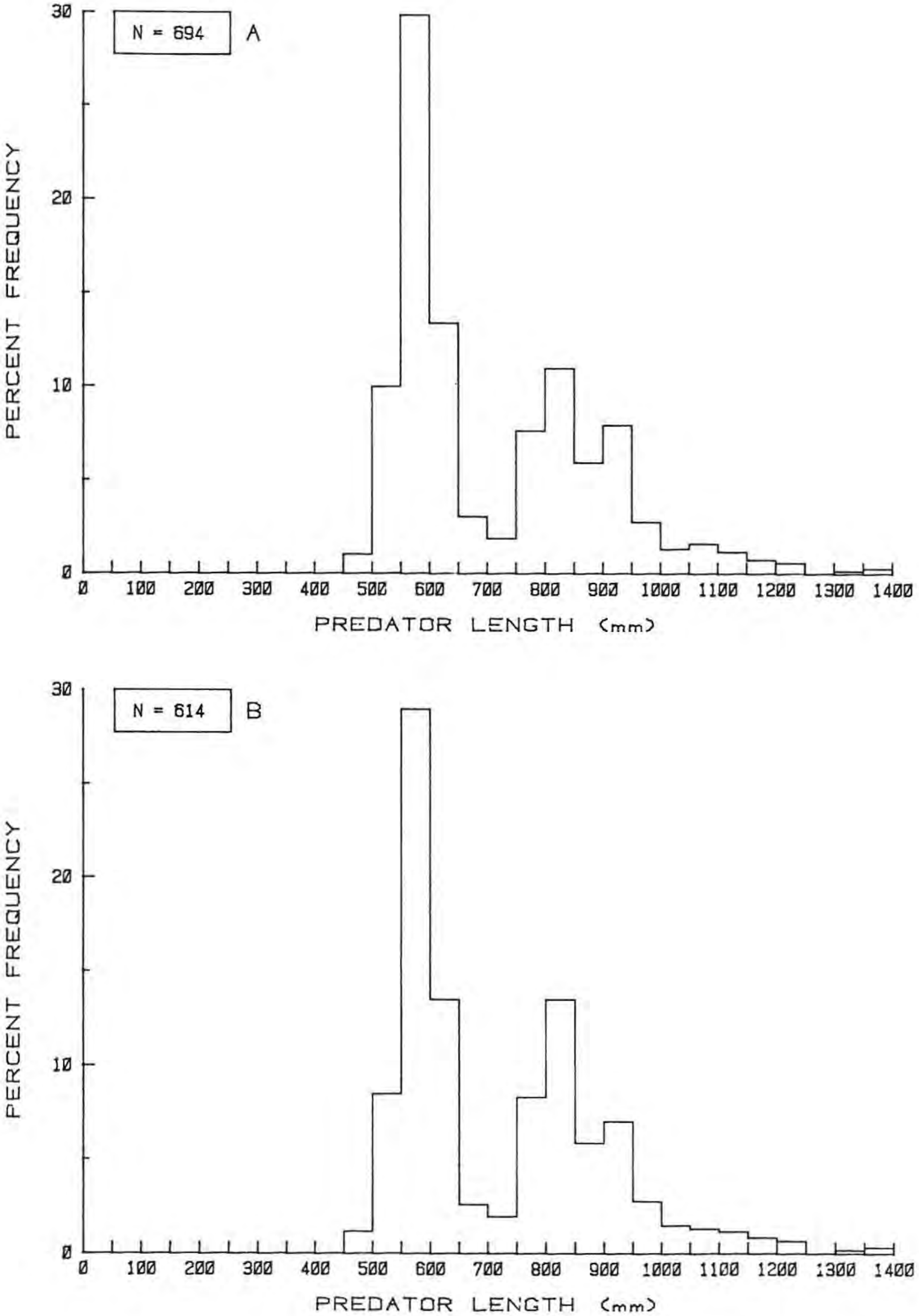


Fig. 25. Histograms of the entire sample of Thunnus albacares (A) and those with stomach contents (B).

Table 14 (a). The prey of *Thunnus albacares* taken inshore < 8 km south of Cape Recife, according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	400 - 600 mm FL			601 - 800 mm FL			801 - 1400 mm FL		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA									
Stomatopoda	3.6	0.6	<0.1	8.9	2.9	0.1	0.9	0.1	<0.1
Euphausiacea				1.6	1.0	0.1			
Megalopa larvae	48.7	53.5	1.5	56.1	56.2	1.4	26.4	19.1	0.2
MOLLUSCA									
Teuthoidea	0.5	0.1	<0.1						
Lolignidae	3.6	2.1	0.2	4.9	0.5	<0.1	0.9	0.2	<0.1
Loligo reynaudi	5.2	0.6	2.1	3.3	0.4	1.2	13.2	1.6	2.6
Ommastrephidae	0.5	0.1	0.7				0.9	0.1	<0.1
Octopoda (Pelagic)	0.5	0.1	<0.1	0.8	0.1	<0.1			
Ocythoe sp.				0.8	0.1	<0.1	0.9	0.1	<0.1
Octopoda (Benthic)							0.9	0.1	<0.1
OSTEICHTHYES									
Unidentified fish	10.4	1.3	2.8	6.5	0.6	<0.1	6.6	0.9	0.1
Clupeidae	0.5	0.1	<0.1						
Etrumeus teres	23.3	6.5	7.7	22.8	4.2	6.0	21.7	7.0	5.9
Sardinops ocellata	45.5	9.3	48.0	45.5	9.4	62.5	64.2	21.2	56.7
Engraulis capensis	46.1	22.0	28.6	43.1	13.8	20.2	43.4	41.7	26.1
Myctophidae				0.8	0.1	<0.1			
Scomberesox saurus	8.8	1.5	6.0	1.6	0.2	0.2	4.7	1.0	2.1
Petalichthys capensis	1.6	0.2	0.7	1.6	0.1	0.3	3.8	0.6	1.6
Priacanthus cruentatus							0.9	0.7	0.4
Carangidae	0.5	0.1	<0.1	0.8	0.1	<0.1			
Trachurus trachurus	3.1	0.6	0.7	3.3	0.2	0.1	2.8	0.2	0.6
Pomadasys olivaceum							0.9	0.1	<0.1
Scomber japonicus	2.1	0.3	0.8	9.8	9.5	7.6	7.5	4.2	3.2
Stomateidae	2.1	0.2	<0.1	1.6	0.1	<0.1			
Coryphaena hippurus							1.9	0.4	0.6
Dactyloptena orientalis	1.0	0.1	<0.1						
Balistidae							1.9	0.1	<0.1
Ostraciontidae	5.2	0.6	0.1	4.1	0.5	<0.1	3.8	0.3	<0.1
Lactoria sp.	0.5	0.1	<0.1	0.8	0.1	<0.1			
Tetrosomus sp.	0.5	0.1	<0.1						
Diodontidae							0.9	0.1	<0.1
Tetraodontidae	0.5	0.1	<0.1				0.9	0.1	<0.1
Lagocephalus sp.				1.6	0.1	0.2			
Totals	193	1621	6795.0	123	1707	7833.5	106	1351	14659.4

Table 14 (b). The Prey of *Thunnus albacares* taken<8 - 40 km south of Cape Recife, according to size. The totals are number of stomach (F), number of items (N) and prey wet mass (M), g.

Prey	400 - 600mm FL %F	%N	%M	601 - 800 mm FL %F	%N	%M	801 - 1400 mm FL %F	%N	%M
CRUSTACEA									
Stomatopoda	33.3	12.0	2.2	21.1	4.8	0.3			
Megalopa larvae	33.3	52.0	7.0	42.1	50.4	1.1	43.8	19.6	0.3
Macrura				5.3	0.4	<0.1			
MOLLUSCA									
Teuthoidea	8.3	1.0	0.5						
Loligo reynaudi	16.7	9.0	0.3	21.1	6.1	12.7	15.7	3.2	1.9
Lycoteuthis diadema	16.7	4.0	3.2	15.7	8.8	14.3	53.1	54.9	22.3
Enoploteuthidae							3.1	0.2	<0.1
Abralia spp.							3.1	0.2	<0.1
Ommastrephidae	16.7	3.0	2.4	10.5	2.6	5.0	25.0	2.6	2.2
Thysanoteuthis sp.				5.3	0.4	2.0			
Onychoteuthidae							3.1	0.2	<0.1
Cranchiidae							3.1	0.2	<0.1
Octopoda (Pelagic)	8.3	1.0	<0.1	5.3	0.9	0.1	9.4	0.9	<0.1
Ocythoe sp.	8.3	2.0	0.5				3.1	0.2	<0.1
Argonauta spp.				5.3	0.4	<0.1			
OSTEICHTHYES									
Unidentified fish	16.7	2.0	9.8	36.8	4.8	21.2	9.4	2.1	0.1
Etrumeus teres	33.3	5.0	54.8	42.1	6.1	31.0	28.1	3.4	12.2
Sardinops ocellata	8.3	1.0	6.9	15.8	1.8	4.8	9.4	1.9	4.9
Engraulis capensis				10.5	8.8	3.3	3.1	0.4	0.1
Myctophidae				5.3	0.4	0.1	9.3	0.6	0.1
Diaphus sp				10.5	0.9	0.5			
Hemirhamphus sp.							3.1	0.2	1.4
Scomberesox saurus				5.3	0.4	2.7	43.8	8.6	54.1
Merluccius capensis							3.1	0.2	<0.1
Carangidae	8.3	1.0	0.5						
Trachurus trachurus				5.3	0.4	0.1	3.1	0.2	0.3
Pterogymnus laniarius	8.3	1.0	6.7						
Balistidae	8.3	4.0	3.7	10.5	0.9	0.6			
Ostracionidae	8.3	1.0	0.2	5.3	0.4	0.1			
Lagocephalus sp	8.3	1.0	1.4						
Totals	12	100	217.5	19	228	1468	32	466	7356

Table 14 (c). The prey of *Thunnus albacares* taken off East London, according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	400 - 600 mm FL %F	%N	%M	601 - 800 mm FL %F	%N	%M	801 - 1400 mm FL %F	%N	%M
CRUSTACEA									
Unidentified crustaceans	2.8	0.4	0.2						
Isopoda	2.8	0.4	<0.1						
Stomatopoda	13.9	6.1	0.8	7.7	0.5	<0.1	5.6	0.6	<0.1
Penaeidea							1.9	0.4	<0.1
Megalopoda larvae	33.3	25.7	1.7	48.7	42.7	2.9	14.8	7.9	0.1
MOLLUSCA									
Gastropoda	2.8	0.4	<0.1	5.1	0.3	<0.1	1.9	0.9	<0.1
Teuthoidea	8.3	1.2	0.3	2.6	0.2	0.1	5.6	0.4	0.2
Loligo reynaudi	5.6	1.2	22.0	5.1	0.3	2.0	3.7	0.3	<0.1
Lycoteuthis diadema							3.7	1.2	<0.1
Ommastrephidae	33.3	14.3	23.9	10.3	1.8	0.2	24.1	7.3	<1.3
Chiroteuthidae	2.8	0.4	<0.1						
Onychoteuthidae	2.8	0.4	0.2						
Octopoda (Pelagic)	11.1	4.9	0.4				3.7	0.5	<0.1
Ocythoe sp.	5.6	1.6	0.1				14.8	1.5	0.4
Argonauta sp.							7.4	1.0	<0.1
Tremoctopus violacea				2.6	0.2	0.1	1.9	0.1	0.5
OSTEICHTYES									
Unidentified fish	25.0	5.7	3.3	7.7	0.5	0.1	16.7	3.4	0.2
Etrumeus teres	27.8	5.3	9.8	20.5	2.4	12.6	35.2	6.2	11.0
Sardinops ocellata				30.8	3.7	26.6	18.5	5.3	18.1
Engraulis capensis	44.4	15.9	33.0	35.9	16.0	23.7	46.3	51.5	26.9
Myctophidae				5.1	0.3	0.1	3.7	0.3	0.2
Diaphus sp.				2.6	11.9	1.9			
Exocoetidae				2.6	0.2	0.8			
Oxyporhamphus sp.	2.8	0.4	<0.1						
Scomberesox saurus				2.6	0.2	1.2	9.3	3.6	24.2
Petalichthys capensis				7.7	0.8	5.3			
Cheilodactylidae				5.1	13.3	2.3			
Priacanthus sp.							1.9	0.1	0.1
Apogonidae				2.6	0.2	0.2			
Carangidae	2.8	0.4	0.1	7.7	0.5	0.2	1.9	0.4	<0.1
Trachurus trachurus	5.6	0.8	0.9						
Euthynnus affinis							1.9	0.1	3.7
Scomber japonicus				25.6	2.1	18.6	22.2	2.1	6.1
Cubiceps sp.				2.6	0.2	0.1			
Stromateidae	5.6	0.8	0.9				3.7	0.5	0.1
Brama orcini							1.9	1.5	6.5
Sphyraenidae				15.4	1.2	0.7	7.4	0.8	0.1
Xiphasia setifer							1.9	0.1	<0.1
Balistidae	2.8	0.4	0.3	5.1	0.3	0.1	3.7	0.3	0.1
Laputa sp.	5.6	0.8	0.5				1.9	0.1	<0.1
Ostraciontidae	19.4	11.4	1.2	2.6	0.2	0.2	5.6	0.6	<0.1
Lactoria sp.	2.8	0.4	0.1	2.6	0.2	<0.1			
Diodontidae				5.1	0.3	0.3			
Cichlichthys sp.	2.8	0.4	0.5				3.7	0.4	<0.1
Tetraodontidae				2.6	0.2	0.1	1.9	0.3	0.2
Lagocephalus sp.							1.9	0.1	<0.1
Molidae							1.9	0.1	<0.1
Totals	36	245	581.1	39	656	2399.8	54	776	9288.3

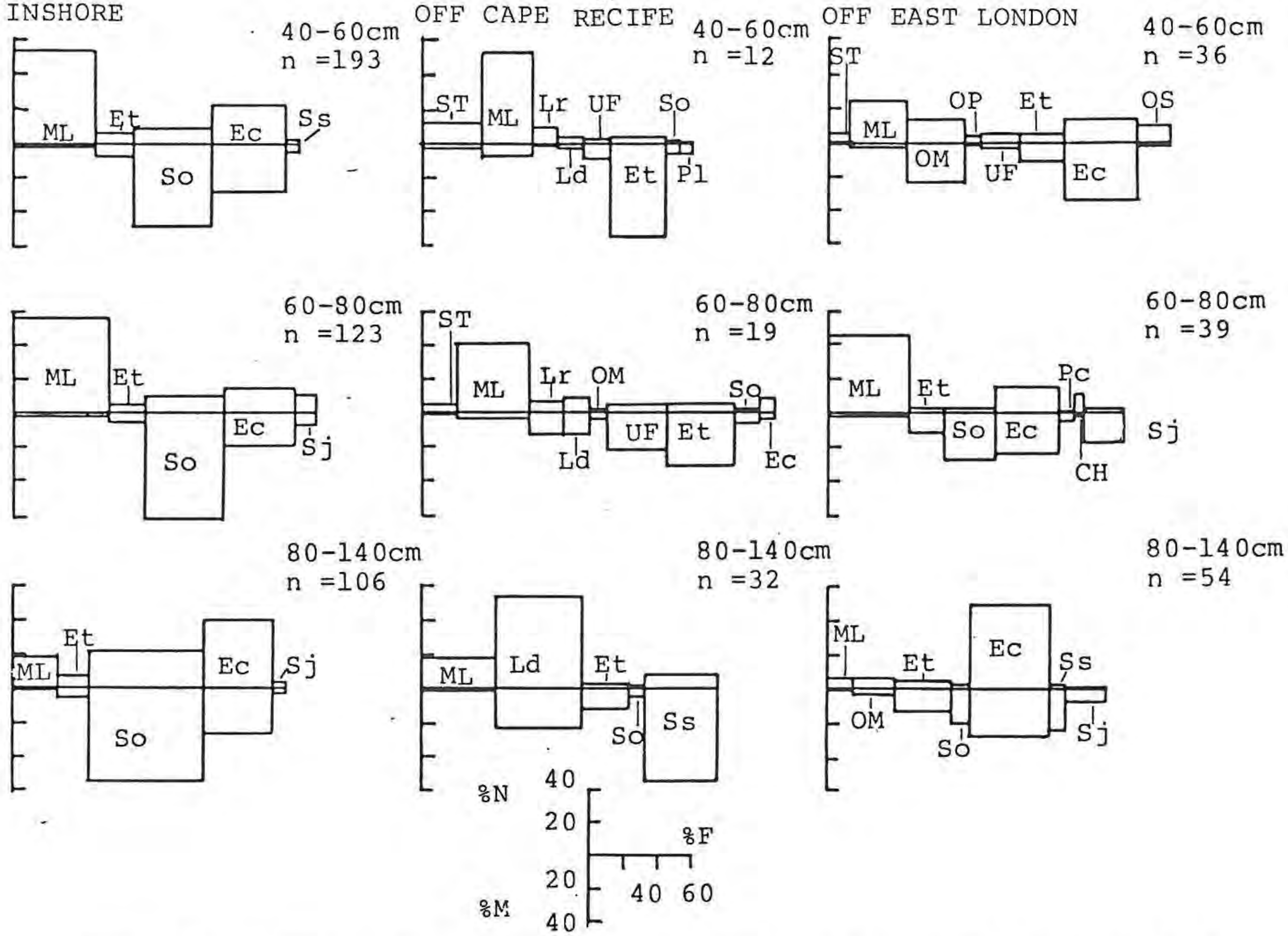


Fig. 26. Principal prey of Thunnus albacares taken inshore (0-8 km), off Cape Recife (8-40 km) and off East London at different sizes.

CH:Cheilodactylidae Ec:Engraulis capensis Et:Etrumeus teres Ld:Lycoteuthis diadema Lr:Loligo reynaudi ML:Megalopa larvae OM:Ommastrephidae OP:Octopoda (Pelagic) OS:Ostraciontidae Pc:Petalichthys capensis Pl:Pterogymnus laniarius Sj:Scomber japonicus So:Sardinops ocellata Ss:Scomberesox saurus ST:Stomatopa UF:Unidentified fish

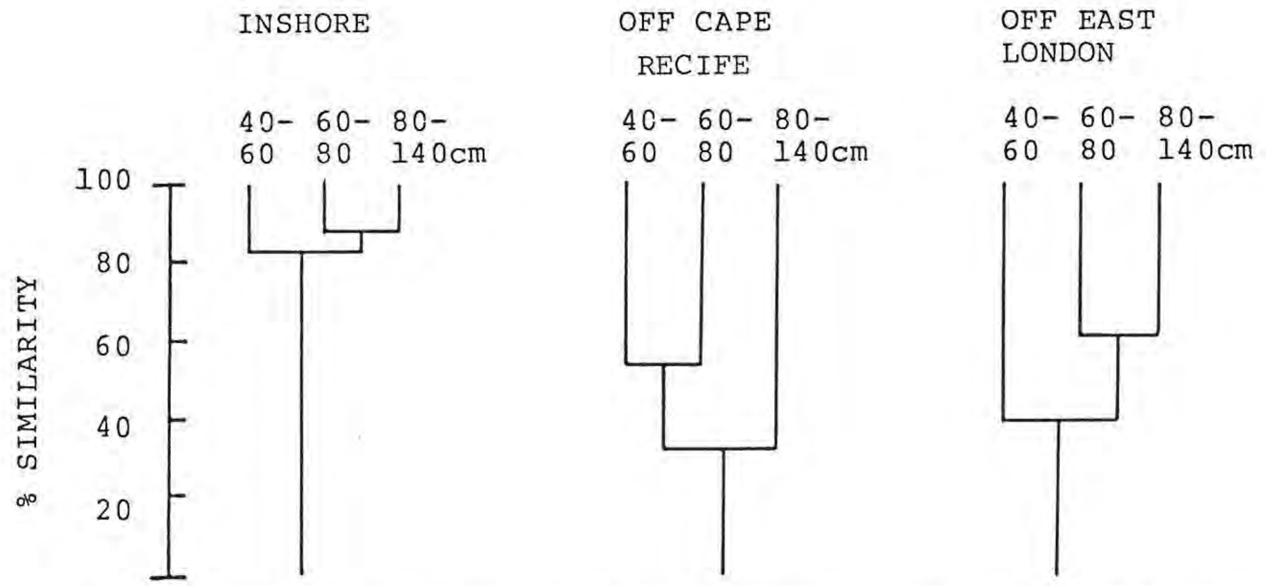


Fig. 27. Similarity dendrograms of diets of Thunnus albacares size groups, according to prey mass. Each was calculated separtely according to locality.

(48%) but less dominant by number (9%). *E. capensis* dominated by number (22%), but was less dominant by mass (29%).

A similar pattern was found with the medium size group (601 - 800 mm). Twenty-one prey types were found in the 123 stomachs collected. Crab megalopae were dominant by frequency and number (56% and 56%) but were less important by mass (1%). The four most important teleost species were *Etrumeus teres*, *S. ocellata*, *Engraulis capensis* and *Scomber japonicus*. *Sardinops ocellata* dominated by mass (63%) but *E. capensis* dominated by number (14%).

The large fish group (801 - 1400 mm) differed from the smaller size groups in the reduction of importance of crab megalopae. The same three teleosts dominated the diet: *Etrumeus teres*, *S. ocellata* and *Engraulis capensis*. *S. ocellata* again dominated by mass (57%) and *E. capensis* by number (42%).

Fewer predators were available from the offshore areas (63). Most were caught from March to May. The 12 small fish (400 - 600 mm FL) took 16 prey types, reflecting a broad selection. Crab megalopae predominate numerically (52%N) and *Etrumeus teres* are dominant by mass (55%M). The 601 - 800 mm FL group also took a wide selection of prey groups. Megalopae dominated numerically. *Loligo reynaudi* and *Lycoteuthis diadema* were important by mass (13% and 14%) although unidentified juvenile fish and *E. teres* dominated by mass (21% and 31%).

Tuna of 801 - 1400 mm also took a variety of prey. Megalopae were less important by number (20%) although they were taken more frequently (44%). Cephalopods were considerably more dominant. *L. diadema* dominated the prey by number (55%) and was taken frequently (53%). The mass contributed was 22%, second only to *S. saurus* (54%). Beak retention was marked. Many of them had only a little adherent flesh, suggesting that they may remain in the stomach longer than other prey. However, the mass contributed suggests they are still important prey items despite this numerical bias. *E. teres* and *Sardinops ocellata* were taken but were dominated by *Scomberesox saurus*.

Off East London the small group was represented by 36 stomachs containing

24 different prey groups. Megalopa were taken and dominated numerically (26%). Ommastrephid squids were the most dominant cephalopod family, making up 14% by number and 24% by mass. Unidentified fish remains were mainly small juveniles. Although Etrumeus teres was taken by this group (28%F, 5%N, 10%M), Engraulis capensis was more dominant (44%F 16%N 33%M). Ostraciontidae were also taken but accounted for only 11% of the number and 1% of the mass of prey.

The 39 yellowfin tuna of 601 - 800 mm took 27 taxa. Megalopae dominated by frequency and number (49% and 43%) but were minor components by mass (3%). The fish component of the diet was dominated by four species: Etrumeus teres, Sardinops ocellata, Engraulis capensis and Scomber japonicus. S. ocellata dominated by mass (27%) and E. capensis by number (16%).

Fifty-four fish with stomach contents between 801 - 1400 mm were collected from East London and contained thirty-three prey taxa. Small crustaceans were taken, but were considerably less important than in the smaller length groups. Brachyuran megalopa larvae occurred in 15% of the stomachs, making up 8% of the prey number. Ommastrephidae occurred in 24% of the sample, making up 7% of the number and 1% of the prey mass. Etrumeus teres, Sardinops ocellata, Engraulis capensis, Scomberesox saurus and Scomber japonicus were the principal prey items by mass and number.

Comparison of the percentage similarity between each of the size classes of T. albacares in the three study areas reveals that inshore the three groups display marked similarity of prey by wet mass. The linkage of the two large groups is slightly higher than the similarity of that pair to the small fish (Fig. 27). This results largely from the very similar diets, dominated by clupeids and engraulids. Offshore, the two smaller groups had more similar diets than did the large group. This was mainly because of the importance of E. teres to both groups whilst the largest group took predominantly Lycoteuthis diadema and S. saurus. Off East London the similarity of the larger fish was attributable to their common predation on E. teres, S. ocellata and E. capensis. In the smaller group Loligo reynaudi and ommastrephids were more important. Their similarity with the large group was mainly a result of their predation on Etrumeus teres and Engraulis capensis.

Predator-prey length relationship

A scatter diagram of prey length against predator length is presented in Fig.28. The relationship varied between 0.3 and 64% of predator length. The size of prey taken was similar over the entire length range of T. albacares although there was a slight increase in the maximum length of prey taken by tuna over 800 mm FL.

The length range of four common prey species taken by the three length groups of T. albacares is shown in Fig. 29. The length range and modes of S. ocellata were very similar for each group. The three size groups show almost complete overlap in prey length ranges and agreement of modal peaks for E. teres and E. capensis which suggests that prey size taken is dependent on availability. The Scomberesox saurus taken measured 208 - 300 mm, 196 - 316 mm and 205 - 460 mm TL respectively for the three tuna groups. From these data it appears that large S. saurus may be unavailable to small T. albacares although the large group of yellowfin will take small S. saurus.

Seasonality of prey selected

There is considerable variation in prey taken between each area, particularly when prey was compared at different times. The principal prey are grouped in bi-monthly periods for all years (Table 15).

In inshore areas, megalopae were present in the first six months but were most numerous in March-April. E. teres occurred in all samples and S. ocellata was dominant early in the year but only of minor importance in November-December. E. capensis was an important component of all sample periods. In the last period S. japonicus dominated the prey.

Offshore of Cape Recife, stomatopods or megalopae were found in large numbers in most samples. Ommastrephids were important only at the beginning and end of the year. Lycoteuthis diadema was important by frequency, number and mass in May-June. E. teres was important by mass in January-February and also in March-April. S. saurus was incidental in January-April but was the major teleost taken in May-June.

Off East London, crab megalopae and stomatopods occurred almost

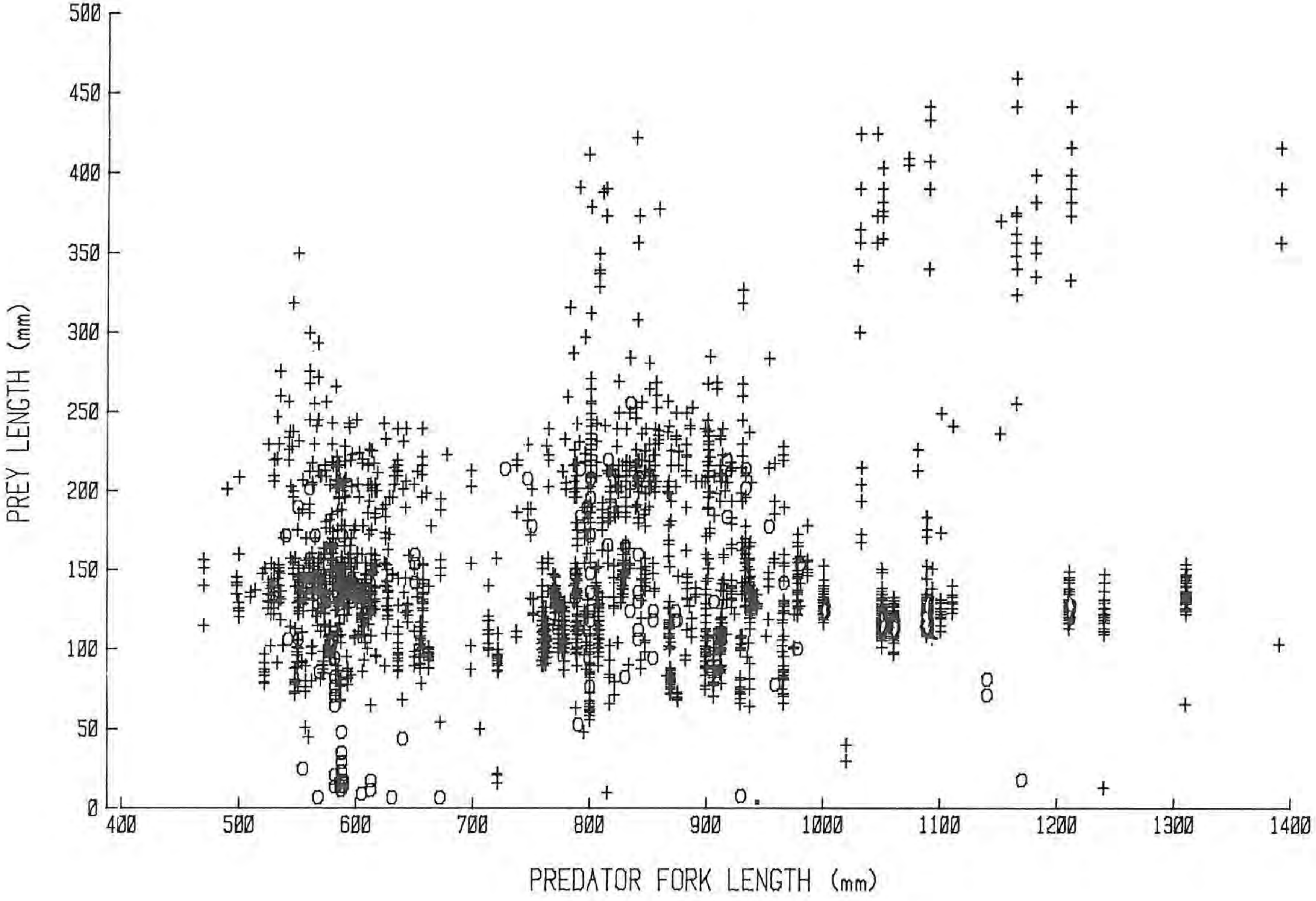


Fig. 28. Scatter diagram of prey length against Thunnus albacares fork length. Crustaceans are shown by dots, cephalopods by circles and fishes by crosses.

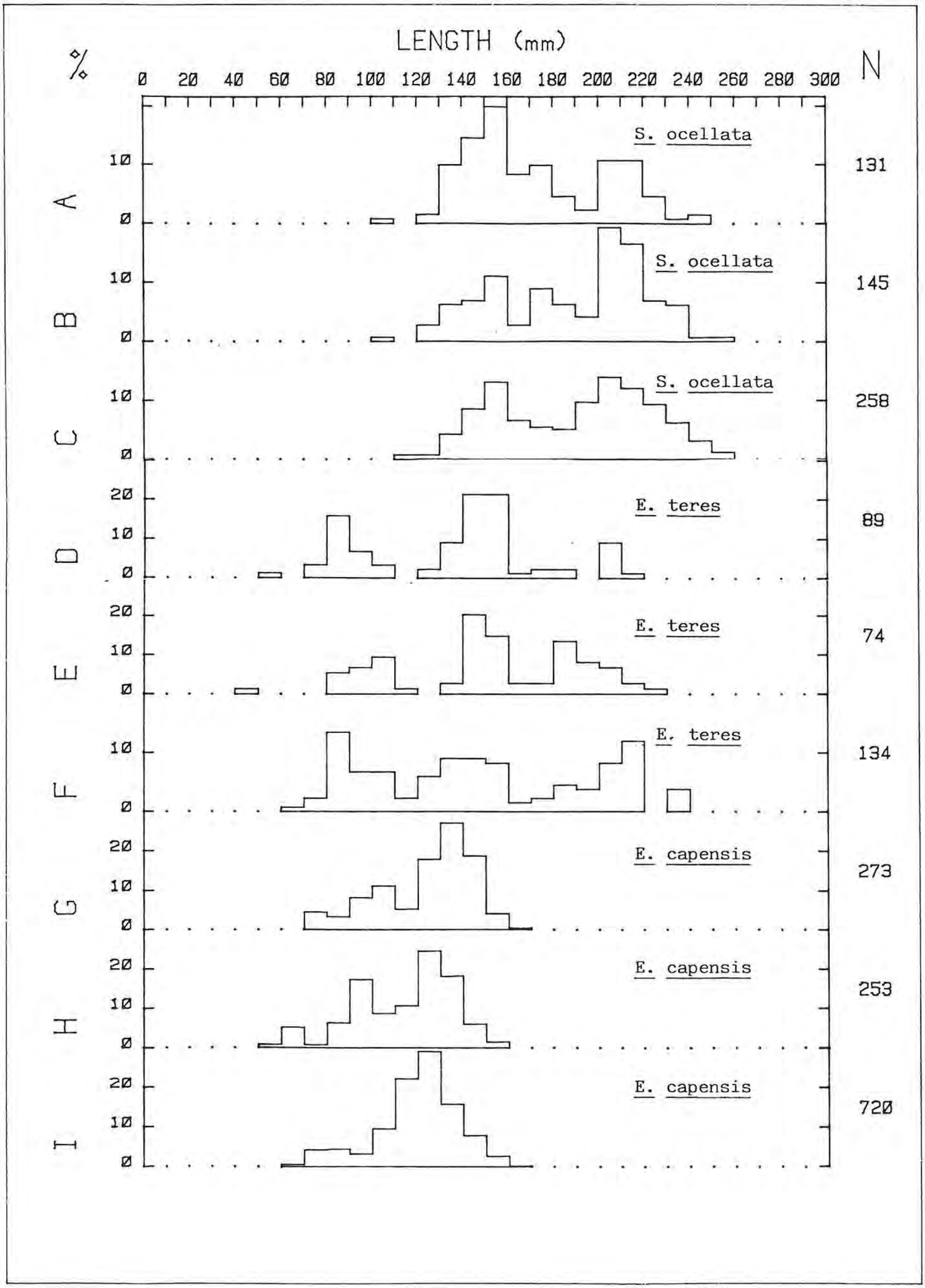


Fig. 29a. Histograms of common prey taken by Thunnus albacares of 400 - 600 mm (A,D,G); 601 - 800 mm (B,E,H) and 801 - 1400 mm (C,F,I). Sardinops ocellata (A,B,C); Etrumeus teres (D,E,F) and Engraulis capensis are shown.

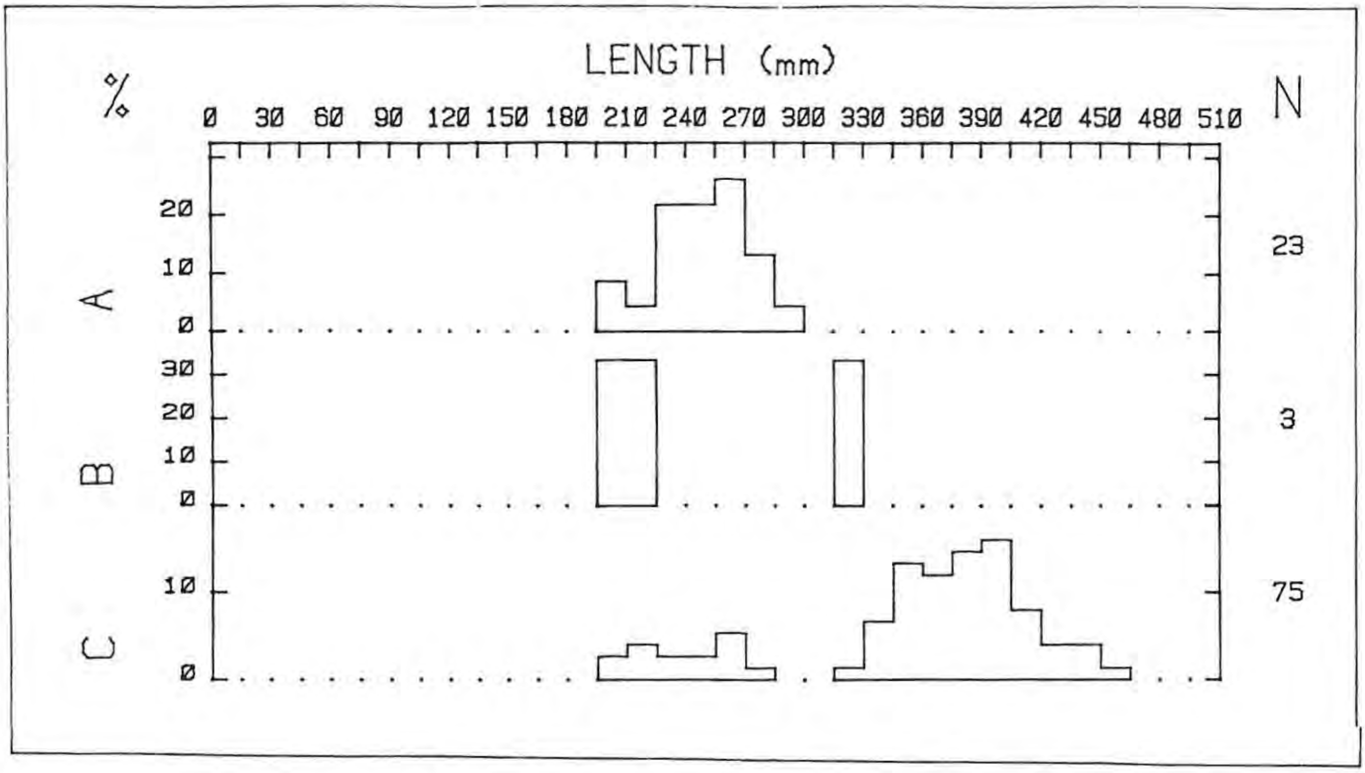


Fig. 29b. Histograms of Scomberesox saurus taken by Thunnus albacares of 400 - 600 mm (A); 601 - 800 mm (B) and 801 - 1400 mm (C).

Table 15 (a). The prey of Thunnus albacares taken in bi-monthly periods in inshore water. The totals are number of stomachs (F), number of items (N) and prey wet mass (M),g.

Prey	January-February			March-April			May-June			November-December		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Stomatopoda				6.8	2.0	0.1						
Euphausiacea				0.7	0.6	<0.1						
Megalopa larvae	41.1	27.2	0.4	48.9	56.6	1.2	37.5	25.0	0.3			
MOLLUSCA												
Teuthoidea				0.4	< 0.1	<0.1						
Lolignidae	1.6	0.8	0.1	4.3	1.1	0.1						
Loligo reynaudi	5.6	0.7	0.7	7.1	0.8	2.9	12.5	5.8	9.5			
Ommastrephidae	0.8	0.1	0.4	0.4	<0.1	<0.1						
Octopoda (Pelagic)				0.7	0.1	<0.1						
Ocythoe sp.				0.7	0.1	<0.1						
Octopoda (Benthic)				0.4	< 0.1	<0.1						
OSTEICHTHYES												
Unidentified fish	7.3	0.7	1.1	8.6	1.0	0.5	12.5	1.9	<0.1	10.0	1.6	<0.1
Clupeidae				0.4	<0.1	<0.1						
Etrumeus teres	21.8	7.8	6.3	23.2	5.2	6.5	12.5	7.7	7.6	30.0	2.0	4.5
Sardinops ocellata	63.7	18.0	59.6	43.9	11.0	56.4	75.0	25.0	69.3	40.0	2.8	4.0
Engraulis capensis	50.8	41.2	28.4	40.0	17.9	24.2	37.5	32.7	9.5	100.0	15.1	13.9
Myctophidae				0.4	<0.1	<0.1						
Scomberesox saurus	4.8	0.7	1.1	6.4	1.1	3.7						
Petalichthys capensis	0.8	0.1	0.3	2.5	0.4	1.6				10.0	0.4	1.0
Priacanthus cruentatus				0.4	0.3	0.3						
Carangidae				0.7	0.1	< 0.1						
Trachurus trachurus	0.8	0.1	<0.1	3.9	0.5	0.8				10.0	0.4	0.3
Pomadasys olivaceum				0.4	<0.1	<0.1						
Scomber japonicus	7.3	1.7	1.5	1.4	0.1	1.0	12.5	1.9	3.8	100	77.8	76.1
Stromateidae				2.1	0.2	<0.1						
Coryphaena hippurus	0.8	0.1	<0.1	0.4	0.2	0.5						
Dactyloptena orientalis				0.7	0.1	<0.1						
Balistidae	0.8	0.1	<0.1	0.4	< 0.1	<0.1						
Ostracionidae	6.5	0.6	0.1	3.9	0.5	<0.1						
Lactoria sp				0.7	0.1	<0.1						
Tetrosomus sp	0.8	0.1	<0.1									
Diodontidae	0.8	0.1	<0.1									
Tetraodontidae				0.7	0.1	<0.1						
Lagocephalus sp.	0.8	0.1	< 0.1	0.4	<0.1	0.1						
Totals	124	1370	11432.4	280	3005	16075.2	8	52	790.4	10	252	990

Table 15 (b). The prey of *Thunnus albacares* taken in bi-monthly periods 8 - 40 km south of Cape Recife. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	January-February			March-April			May-June			November-December		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Stomatopoda	33.3	26.7	0.1	15.0	4.2	0.2	5.9	0.3	0.1			
Megalopa larvae				32.5	42.3	1.3	70.6	22.6	0.3	33.3	5.6	0.5
Macrura				2.5	0.2	<0.1						
MOLLUSCA												
Teuthoidea	33.3	6.7	0.3									
Loligo reynaudi				25.0	7.4	10.4	5.9	1.8	0.7			
Lycoteuthis diadema				15.0	19.9	2.8	94.1	59.1	30.1			
Enoploteuthidae							5.9	0.3	<0.1			
Abralia sp.				2.5	0.2	0.1						
Ommastrephidae	100	26.7	2.1	7.5	1.2	1.0	29.4	2.1	3.3	33.3	27.8	45.5
Thysanoteuthis sp.				2.5	0.2	1.1						
Onychoteuthidae							5.9	0.3	<0.1			
Cranchidae							5.9	0.3	<0.1			
Octopoda (Pelagic)				5.0	0.7	0.1	17.6	1.2	0.1			
Ocythoe sp.							5.9	0.3	0.1	33.3	11.1	4.5
Argonauta spp.				2.5	0.2	<0.1						
OSTEICHTHYES												
Unidentified fish				22.5	3.0	12.2	5.9	0.3	<0.1	66.7	50.0	45.0
Etrumeus teres	33.3	26.7	88.4	47.5	6.9	38.5	5.9	0.3	1.5			
Sardinops ocellata	33.3	6.7	3.9	15.0	3.0	15.9						
Engraulis capensis				7.5	5.1	2.0						
Myctophidae				5.0	0.5	0.3	5.9	0.3	<0.1	33.3	5.6	4.5
Diaphus sp.				5.0	0.5	0.3						
Hemirhamphus sp.				2.5	0.2	3.7						
Scomberesox saurus	33.3	6.7	5.2	12.5	1.2	7.8	52.9	10.7	63.9			
Merluccius capensis				2.5	0.2	<0.1						
Carangidae				2.5	0.2	<0.1						
Trachurus trachurus				5.0	0.5	0.9						
Pterogymnus laniarius				2.5	0.2	0.5						
Balistidae				7.5	1.4	0.6						
Ostracionidae				5.0	0.5	0.1						
Lagocephalus sp.				2.5	0.2	0.1						
Totals	3	15	384.5	40	433	2712	17	328	5923	3	18	22

Table 15 (c). The prey of *Thunnus albacares* taken in bi-monthly periods off East London. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

	January-February			March-April			May-June			July-August			September-October			November-December		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA																		
Unidentified crustaceans				14.3	1.9	1.5												
Isopoda				14.3	1.9	0.2												
Stomatopoda	4.8	0.5	<0.1	42.9	20.4	5.9	9.1	0.7	<0.1	18.2	7.0	0.1				2.2	0.4	<0.1
Penaeidea																2.2	0.4	0.1
Megalopa larvae	33.3	13.9	0.3	28.6	7.4	1.1	52.3	56.6	1.2							15.6	5.3	0.2
MOLLUSCA																		
Gastropoda	4.8	0.5	<0.1	14.3	1.9	0.2	2.3	1.2	<0.1							2.2	0.1	<0.1
Teuthoidea	4.8	0.5	0.2	42.9	5.6	2.3				18.2	3.5	2.0				2.2	0.1	<0.1
Loligo reynaudi	4.8	0.5	<0.1				4.5	0.3	0.7	9.1	1.8	0.1				4.4	0.4	4.0
Lycoteuthis diadema	9.5	4.3	0.2															
Ommastrephidae	9.5	1.0	<0.1	42.9	13.0	8.3	6.8	0.5	1.1							46.7	11.9	5.8
Chiroteuthidae																2.2	0.1	<0.1
Onychoteuthidae				14.3	1.9	1.5												
Octopoda (Pelagic)	4.8	0.5	<0.1	28.6	16.7	2.9										·6.7	0.8	0.1
Ocythoe sp.	4.8	0.5	<0.1							27.3	5.3	0.2				13.3	1.6	1.0
Argonauta sp.	4.8	0.5	<0.1													6.7	0.9	0.1
Tremoctopus violacea																4.4	0.3	1.4
OSTEICHTHYES																		
Unidentified fish	19.0	1.9	0.2	42.9	13.0	5.3	6.8	0.5	0.1							24.4	3.7	0.8
Etrumeus teres	23.8	2.9	5.9				20.5	3.3	7.9	81.8	47.4	61.7				31.1	3.2	4.6
Sardinops ocellata							47.7	11.0	34.8							2.2	0.1	<0.1
Engraulis capensis	52.4	58.2	90.1	28.6	11.1	60.2	34.1	12.7	3.8	9.1	10.5	0.1				57.8	43.5	55.8
Myctophidae							9.1	0.7	0.3									
Diaphus sp.																2.2	10.1	1.4
Exocoetidae							2.3	0.2	0.3									
Oxyporhamphus sp.																2.2	0.1	<0.1
Scomberesox saurus							11.4	4.8	33.7							2.2	0.1	0.9
Petalichthys capensis							2.3	0.3	0.9	9.1	1.8	4.5				2.2	0.3	0.6
Cheilodactylidae																4.4	11.2	1.7
Priacanthus sp.	4.8	0.5	0.4															
Apogonidae							2.3	0.2	0.1									
Carangidae	4.8	0.5	<0.1				4.5	0.3	<0.1	18.2	7.0	0.3						
Trachurus trachurus	4.8	0.5	<0.1	14.3	1.9	7.5												
Euthynnus affinis							2.3	0.2	5.1									
Scomber japonicus	4.8	0.5	0.8				29.5	3.3	9.2	54.5	14.0	31.0				4.4	0.3	2.4
Cubiceps sp.																2.2	0.1	<0.1
Stromateidae	14.3	2.4	0.6													2.2	0.1	0.1
Brama orcini																2.2	1.6	18.7
Sphyraenidae							22.7	2.2	0.4									
Xiphasia setifer	4.8	0.5	0.1															
Balistidae	4.8	0.5	<0.1	14.3	1.9	3.0	6.8	0.5	0.1									
Laputa sp.	14.3	1.4	0.3															
Ostraciontidae	19.0	7.2	0.3	14.3	1.9	0.5				9.1	1.8	<0.1	100	100	100	8.9	2.1	0.1
Lactoria sp.																4.4	0.3	<0.1
Diodontidae	4.8	0.5	0.5													2.2	0.1	<0.1
Ciclichthys sp.																6.7	0.5	0.2
Tetraodintidae							4.5	0.5	0.3									
Lagocephalus sp.																2.2	0.1	0.1
Molidae																2.2	0.1	0.1
Totals	21	208	1302.3	7	54	66.6	44	583	6654.3	11	57	1025	1	1	4.5	45	774	3215.5

throughout the year. Lycoteuthis diadema was recorded only in January-February, but another squid family, the Ommastrephidae, occurred in the first three periods and the last. Etrumeus teres dominated other prey in July-August. E. capensis dominated the prey at the begining and end of the year. S. ocellata was again important in May-June, as was found in K. pelamis.

Annual variation

The annual variation of prey taken by T. albacares from inshore areas is presented in Table 16. Fluctuations in importance of minor prey species are probably a result of normal variation. The most notable change of major prey items is that S. ocellata decreases in importance after 1978. Conversely, Engraulis capensis increases in importance after 1978 while Etrumeus teres is relatively more important in 1979.

Stomach fullness indices

The maximum feeding index of T. albacares was 5.5% of body mass and a mean of 0.9% (n=614) was recorded. A mean reconstituted stomach mass of 1.7% (n=590) body mass and a maximum value of 17.7% was recorded.

Discussion

T. albacares examined during this study ranged from 452 - 1390 mm, which is lower than the range sampled by long-line off the South African west coast (820 - 1550 mm, Nepgen 1970). Williams (1966) recorded a range of 625 - 1640 mm off East Africa in an exploratory long-lining operation. The tendency for sub-surface fisheries to catch larger tunny has frequently been noted (Reintjies & King 1953, Blackburn 1965, Talbot & Penrith 1968). This is thought to be related to the swimming depth of various sizes of tuna (Talbot & Penrith 1968) which may be found from the surface to approximately 150 m (Blackburn 1965), although a recent paper by Kornilova (1980) describes the diet of yellowfin caught down to depths of 265 m. Regrettably no account of depth recording is given and it is not clear if this depth was assumed from the lengths of the line. If so the records are dubious as lines are known to bow and stream (Blackburn 1965, Talbot & Penrith 1968). Cole (1980) quotes an unpublished manuscript by Miller & Evans which reported that strong thermocline gradients and dissolved oxygen concentrations less than 2 ml/l below the thermocline appear to present a barrier to yellowfin. Thus local oceanographic conditions of temperature and oxygen may limit depth distribution.

Table 16. The prey of *Thunnus albacares* taken from Algoa Bay and environs in different years of the study. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

	1978			1979			1980			1981		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Stomatopoda	8.7	4.0	0.1	6.7	1.6	<0.1	0.7	0.1	<0.1			
Euphaustacea	8.7	5.3	<0.1									
Megalopa larvae	34.8	46.3	0.9	53.8	53.3	1.3	33.6	31.3	0.4	55.6	40.5	0.8
MOLLUSCA												
Teuthoidea				0.4	<0.1	<0.1						
Loliginidae				5.4	1.5	0.1				11.1	2.7	0.4
Loligo reynaudi	8.7	1.2	2.4	7.1	0.6	3.7	4.1	0.9	0.5	22.2	4.1	0.5
Ommastrephidae				0.4	<0.1	<0.1	0.7	0.1	0.4			
Octopoda (Pelagic)				0.8	0.1	<0.1						
Ocythoe sp				0.8	0.1	<0.1						
Octopoda (Benthic)				0.4	<0.1	<0.1						
OSTEICHTHYES												
Unidentified fish	8.7	0.6	<0.1	9.6	0.9	0.6	6.2	2.3	1.1	11.1	1.4	0.1
Clupeidae				0.4	<0.1	<0.1						
Etrumeus teres	13.0	4.3	2.0	30.0	6.4	10.1	11.6	3.9	1.2	11.1	2.7	0.1
Sardinops ocellata	60.9	32.6	87.5	42.5	7.6	46.2	61	22.8	67.4	55.6	10.8	68.3
Engraulis capensis	13.0	2.8	1.3	47.9	19.0	28.1	43.8	33.2	20.0	22.2	23.0	17.2
Myctophidae	4.3	0.3	0.1									
Scomeresox saurus				4.2	0.4	2.1	9.6	2.7	4.3			
Petalichtys capensis	8.7	1.9	4.3	0.8	0.1	0.1	3.4	0.5	1.2			
Priacanthus cruentatus										11.1	12.2	12.0
Carangidae				0.8	0.1	<0.1						
Trachurus trachurus				5.0	0.5	1.1	0.7	0.1	0.1			
Pomadasys olivaceum							0.7	0.1	0.1			
Scomber japonicus	4.3	0.3	0.9	5.0	6.7	6.3	6.2	1.8	2.6			
Stomateidae				2.5	0.2	<0.1						
Coryphaena hippurus							1.4	0.6	0.8			
Dactyloptena orientalis				0.8	0.1	<0.1						
Balistidae				0.4	0.1	<0.1	0.7	<0.1	<0.1			
Ostraciontidae				5.0	0.5	<0.1	4.1	0.6	0.1	11.1	1.4	0.4
Lactoria sp				0.8	0.1	<0.1						
Tetrosomus sp							0.7	0.1	<0.1			
Diodontidae				0.4	<0.1	<0.1						
Tetraodontidae				0.8	0.1	<0.1						
Lagocephalus sp	4.3	0.3	0.4							11.1	1.4	0.1
Totals	23	322	3256.6	240	2940	12397.9	146	1079	11087.2	9	74	453.2

T. albacares has been recorded from late October to early August on the Cape west coast and from mid August to late March on the Cape east coast (Talbot & Penrith 1968). However, during the current study they were recorded from December to April in Algoa Bay. Furthermore, records kept by the Port Elizabeth Deepsea Club indicate that this species may be caught offshore (8 - 40 km south of Cape Recife) throughout the year, but appear to be most abundant from May to July. However, their appearance and abundance is very variable and unpredictable, the reason for which is unclear. Water temperature may have an influence although Sharp (1978) notes that relationships between the environment and the behavioural responses of tuna schools or individuals remain obscure.

Yellowfin tuna are caught over a wide temperature range off the western Cape. Talbot & Penrith (1968) recorded T. albacares in water of 13.8° - 24°C whilst Nepgen (1970) recorded tuna from 15° - 21°C, with an optimal temperature of 18° - 21°C. Kishinouye (1923) records a range of 14° - 27°C and an optimum range of 22° - 24°C. Such records suggest a wide temperature range for T. albacares. Off the eastern Cape the species is normally encountered when surface temperatures are above 20°C and frequently in clear water. Their occurrence inshore appears to be related in part to the temperature of the coastal waters, but the unpredictability of their occurrence suggests that other factors are also involved.

The origin of the local population is uncertain. There is no evidence that T. albacares breeds off the Cape coast (de Jager et al. 1963, Talbot & Penrith 1968, Nepgen 1970 and pers. obs.), although some of the yellowfin showed early stages of gonadal maturation in Spring (de Jager et al. 1963). Warm uniform conditions are thought to be necessary for spawning, with temperatures of 24°C or higher (Yabe et al. 1963) but such conditions are not encountered off the Cape. The species is known to occur in the Atlantic Ocean off Angola and also in the western Indian Ocean off Natal and East Africa although Talbot & Penrith (1968) suggest that the origin of the Cape population is in the Indian Ocean. Williams (1962) recorded yellowfin off East Africa throughout the year but noted a marked increase in numbers at the end of the south-east monsoon and during the north-east monsoon (approximately October to March). Waters off East Africa are believed to be a spawning ground for these fish which were ripe-running in October-November and spent in July, October and November.

Talbot & Penrith's (1968) work suggests that their occurrence in the eastern Cape may be transitory, but the study of ski-boat catches suggests a more prolonged stay in inshore waters from about December to May, although the time of their arrival and departure appears to be highly variable. Such a prolonged stay could in fact be a repeated passage through eastern Cape waters by several temporally disjunct schools. It is also possible that schools stay in one area, for example Algoa Bay, for more prolonged periods - days or even weeks. This question could be resolved by an intensive tagging programme. Their stay in coastal areas would be governed by both the suitability of the water mass (e.g. temperature, water clarity, oxygen, salinity) and the availability of suitable prey, namely pelagic fishes or squid.

This study has illustrated the dominance of *S. ocellata* and *E. capensis* in the diet of nearshore yellowfin tuna. It is noteworthy that *Loligo reynaudi* is not a principal prey of *L. albacares* inshore even though other species do take *T. reynaudi* (e.g. *A. hololepidotus*, *P. saltatrix*, *S. lalandi*). This suggests that shoaling fish are preferred prey of *T. albacares*, perhaps because of their higher energy values (Batchelor 1982). Offshore *T. albacares* are frequently caught close to the edge of the continental shelf, alongside the Agulhas Current. In this area different species were shown to dominate the diet: *E. teres*, *Scomberesox saurus* and squids, especially *L. diadema* and ommastrephids. The change of diet with locality effectively reduces the predatory impact of this species on coastal schooling fishes and reduces the potential for competition both intra- and interspecifically. This was reflected by lower similarities of the predator size-groups offshore. Similarly a variation in diet was demonstrated off East London which strongly suggests that *T. albacares* is feeding according to prey availability. The fact that a large size range of prey is taken, from small crab megalopae to pelagic schooling fishes, further indicates the plasticity of the diet and suggests opportunistic feeding, although characteristically a few items appear to be dominant for a given region (Reintjies & King 1953, Williams 1966, Dragovich 1971, Dragovich & Pothoff 1972). *T. albacares* and *K. pelamis* off East London take some prey which are very similar to those found in more northern parts of the Indian Ocean (Williams 1966, Kornilova 1980) which indiates the influence of tropical water here. The teleosts taken show that yellowfin tuna often feed in surface waters, taking Ostraciontidae and other species associated with flotsam, and surface dwelling fish such as S. saurus.

Examination of the cephalopods taken by T. albacares revealed that 16 taxa were recorded. In most cases it was not possible to identify prey to species level except when either beaks were very distinctive or when whole undigested specimens were recovered. Most were epipelagic, occurring in water shallower than 200 m, or neritic (e.g. Loligo, Lycoteuthis, Ommastrephidae, Onychoteuthis, Ocythoe, Argonauta) (Clarke 1966, Voss 1967a, Roper & Young 1975.). Some prey were not restricted to this depth and may be found down to 800 m (e.g. Onychoteuthis) or 1000 m (e.g. Ommastrephidae, Clarke 1966), although ommastrephids are frequently caught at the surface at night, often occurring in large shoals (Wormuth 1976). Other prey groups may live considerably deeper e.g. the Cranchiidae, a complex group which exhibits several different patterns of vertical distribution (Roper & Young 1975). It is difficult to form a clear picture of depth distribution of squid prey, partly because of the intrinsic complexity of their vertical distribution patterns and the difficulty in collecting material, and partly because confident identification to species level has often not been possible. Accurate identification may be possible in future with the development of sophisticated biometric methods which are useful in identifying squid beaks (Wolff & Wormurth 1979, Wolff 1982).

Lycoteuthis diadema was identified from whole specimens (by M. Roeleveld pers.comm.) and from their very characteristic beaks. Voss (1962) has recorded L.diadema in open net trawls fished to depth of 366 - 3000 m. Juveniles have been recorded from 46 - 57 m. Voss (1967b) also recorded a female of 38.6 mm mantle length from west of Slangkop in 350 m and a juvenile measuring 12.3 mm mantle length from west by south of Slangkop in 250 m, and suggested that it inhabited the mesopelagic zone in cool waters, apparently worldwide. The depth distribution is not exactly clear, however, as his material was collected with an open net which collects both at a maximum depth and during ascent and descent. Depth distribution is further complicated in pelagic squid as many exhibit a vertical migration (Voss 1967a). Voss (1967a) considers Lycoteuthis to be a small active swimming mesopelagic species. Ross (1979) found that

Lycoteuthis diadema (which he called *Oregoniateuthis*) is ammoniacal which suggests that they may not be as active as ommastrephid squids (Clarke *et al*. 1979). *L. diadema* becomes a steadily more important prey item of larger yellowfin tuna, which suggests that the larger fish feed more often in deep water than do smaller conspecifics. This finding agrees with previous studies on depth distribution of yellowfin (e.g. Reintjies & King 1953, Williams 1962, Blackburn 1965, Suda 1973). Furthermore, Kishinouye (1923) records diurnal changes in depth distribition. Tuna swim at shallower depths at night, probably following movements of the plankton and intermediate predators. *Lycoteuthis diadema* were rarely encountered in this study off East London, probably because it is a cool water species. *L. diadema* may be rare or even absent but beaks could be transported by the fast-swimming tuna. Alternatively it may occur in deeper cool waters not exploited by *T. albacares*. A notable difference between the fish taken from East London and those collected offshore of Port Elizabeth is that small tuna took considerably more cephalopods off East London while the largest fish took more schooling pelagic fish. This is probably because samples from close inshore and the edge of the continental shelf were mixed. The neritic *L. reynaudi* made up 22% by mass of the small tuna's diet. Ommastrephidae were also found to be important, especially to the small group. The importance of Ommastrephidae in the diet of *T. albacares* has been noted previously (Williams 1966, Perrin *et al*. 1973, Wolff 1982) and this is probably related to their abundance in a particular area (Perrin *et al*. 1973).

The highly productive Cape coastal waters (Finenko 1978) with their associated clupeids and engraulids (Crawford 1981a,b,c) provide a rich feeding ground for yellowfin during summer and may be the cause of tuna migrations to temperate waters. Previous authors (Blackburn 1969, Murphy & Shomura 1972, Uda 1973) have also suggested that prey distribution is an important factor in tuna distribution. The mean fullness index recorded in this study (0.9%) is higher than those recorded by Kornilova (1980) in the central Indian Ocean (0.2% - 0.4%), possibly suggesting a higher feeding rate and higher prey availability in the Cape. This interpretation may not be entirely valid however, as Kornilova does not give details of his calculation methods in his paper and, even if identical, the sampling methods are different (longline versus surface trolling). This would probably result in differences in stomach fullness as ski-boat anglers actively search for surface-feeding schools. Differences in depths of capture between the two studies would also influence regurgitation. The similarity of the mean feeding indices of K. pelamis and T. albacares is striking although the higher consumption index of T. albacares is attributable to squid beak retention and could represent food intake over one day if yellowfin feed in a similar way to skipjack (Magnuson 1969).

Discussion of pelagic predators and their prey.

The prey of the six common teleost pelagic predators has been discussed for each species and for differences in predator size, locality and time. In the following discussion predators will be compared and the behavioural interactions of predator and prey will be discussed. The principal prey species are also important commercial trawl fish. Their occurrence in the eastern Cape will be examined in relation to their known distribution and age structure in the South African west coast pelagic fishery. Finally, other predators of pelagic fishes will be described. They include three teleosts which were rarely sampled in this study. Others, including sharks, birds and marine mammals, will also be discussed.

Anatomical similarities

All the pelagic predators examined shared several anatomical features, reflecting covergent evolution in several families to a pelagic mode of life. The ideal fusiform body is most closely approached by tunas (Lagler et al. 1977). The other predators are more elongate, lacking the narrow keeled caudal peduncle and finlets of the tunas. In P. saltatrix and L. amia, the body is laterally compressed, probably reflecting their hunting in the shallows and around reefs where a deep body increases manoeuvrability and may also assist in thrust generation (Gosline 1971, Webb & Keyes 1981).

All the species have strongly forked or crescent-shaped tails. Colour varies from grey-green in P. saltatrix and L. amia to silvery grey in A. aequidens, probably providing the best camouflage in their near-shore and relatively turbid environment. The blue dorsal and white ventral colouration of tunas is an adaptation for clear oceanic water and similar colouration suggests that S. lalandi may also prefer clean water.

All the fish have relatively fine, backwardly directed teeth which aid ingestion of relatively small prey. *A. aequidens* has slightly larger teeth, probably because of its sciaenid phylogeny. *P. saltatrix* on the other hand has sharp cutting teeth.

In summary, these features are highly evolved to enable predators to cover long distances not only for hunting patches of prey but also for migrating. Finally, they enable predators to outpace their prey during feeding attacks (Major 1978, Hobson 1979). Such anatomical adaptations are similar to those of tropical reef water column foragers (Davis & Birdsong 1973) although in this case speed may be used more for escape from predators.

Physiological adaptations

A notable difference between tunas and inshore pelagic predators is the elevated body temperatures maintained by the *retia mirabila* (Barrett & Hester 1964, Carey *et al*. 1971, Carey 1973) although heat exchangers of *K. pelamis* differ in structure to those of *T. albacares* (Carey & Teal 1966, Graham 1975, Graham & Diener 1978, Sharp & Vlymen 1978). The advantages of elevated body temperature include enhanced vision for prey detection, increased basal swimming and burst speeds (Yuen 1966, Graham 1975, Magnuson 1978) and rapid recovery after exercise to allow frequent feeding frenzies (Stevens & Neill 1978). The elevated body temperature also allows sensing of weak temperature gradients (Neill *et al*. 1976) and movements through the thermocline (Graham 1975, Neill *et al*. 1976). Because of their high metabolic activity they need to feed at high rates. In yellowfin but not skipjack the swimbladder develops as body mass increases, aiding buoyancy and reducing the necessity for high speed swimming for lift (Magnuson 1973, Sharp & Vlymen 1978) thus helping to conserve energy.

Pelagic prey and schooling

Pelagic schooling fishes and squid have been shown to dominate in the diets of all the pelagic predators.

As described below, pelagic fish and squid are patchily distributed but extremely abundant, and form the basis of an important trawling industry in the western Cape. The pelagic predators are able to exploit this rich resource, possibly feeding in a density-dependent way. This has frequently been found for a wide variety of fish predators (e.g. Pinkas _et al_. 1971, Whitfield & Blaber 1978, Bruton 1979, Kok 1980, Medved & Marshall 1981).

However, exploitation of this prey resource is not straightforward. The prey have become highly specialised to protect themselves from predation and a principal tactic appears to be schooling. Because of the importance of this behaviour, the advantages of schooling will be discussed and some recent observations on predator behaviour will be described. Finally the interactions of several co-occurring predators will be examined, and the possibility that co-operation between species may give the predator an advantage will be discussed.

Schooling has been examined in the field (e.g. Hobson 1968, 1972, 1973, Potts 1969, 1970) and tested experimentally (Neill & Cullen 1974, Major 1978, Pitcher & Partridge 1979, Partridge _et al_. 1980). Models (e.g. Treisman 1975a,b, Breder 1976) have also provided a wealth of new information and interpretations on schooling. Recent reviews of schooling are provided by Shaw (1970, 1978), Radakov (1973) and Keenleyside (1979)

Grouped prey are less likely to be detected than scattered individuals as their 'spheres of visibility' to predators overlap (Brock & Riffenberg 1960, Partridge 1982). This advantage is enhanced in water in which physical properties cause light reflection, scattering and absorption. Even in very clear water an object, irrespective of size, is not visible at 70 m (Brock & Riffenberg 1960). This sets a finite distance beyond which prey will not be seen. Naturally this distance will be considerably less in turbid water. Most openwater and reef predators are visual hunters at close distance (Hobson 1963, 1968, Potts 1970, Hartline _et al_ 1972, Potts 1980) although they may use other sensory detection at long distance, for example scent (Hobson 1963) and sound (Richard 1969, Banner 1972).

Models predict that grouped prey have a reduced kill rate in large schools (Treisman 1975a). However, in reality predators are likely to be able to determine the most probable location of prey from their depth and temperature preferences. Concentrated search patterns in areas likely to support prey would therefore reduce the benefit of concealment to schooling prey (Curio 1976). Theoretically, large predators could follow a school, preying on it until extinction. How this is avoided is unknown and merits research. Sonic tagging of predators (Carey & Robinson 1981, Carey *et al*. 1982) and following prey schools with sonar may resolve the question for midwater prey. Long-term observational studies (e.g. Hobson 1968, 1972, 1973, 1974) also deserve further attention.

Another advantage in grouping is improved surveillance for predators thereby allowing time for avoidance (Bowen 1931, Orians 1971, Hobson 1978). Once a predator has been detected the school members move closer together and become more alert (Hobson 1968, Potts 1970, 1980, 1981, Potts (1970, 1980, 1981) studied the interactions of *Caranx* and its prey and showed that the prey response is marked when a specific type of predator approaches and that the predator's size distinctly influences the intensity of the 'fright' behaviour. The advantage of closing ranks is believed to provide a 'confusion effect' when the predator attacks. Visual confusion occurs when several prey are seen simultaneously. The predator has difficulty in concentrating on one particular prey, especially as members move away from the source of disturbance, often opening up to allow the predator to pass through in a 'fountain effect', then reforming behind the advancing predator (Hobson 1968, Potts 1970, Nursall 1973, Radakov 1973). The tactic is most effective with relatively large prey which need to be specifically chosen and not filtered from a school. Neill & Cullen (1974) confirmed these ideas for both fish and cephalopod predators experimentally, finding a lower capture-contact ratio with increased prey numbers. Radakov (1973) obtained a similar result with cod, which captured individual prey in a fraction of the time needed to take schooling prey (26 sec. and 135 sec. respectively). Major (1978) confirmed these findings and noted that lone predators concentrated their attacks on individuals away from the school. Early observations on predation of particularly compact schools of active fish led Springer (1957) to suggest that the school appears to be formidable to predators. However this interpretation seems unlikely from further field work (Hobson 1968). Predators are reluctant to attack schools probably because of a conflict between attacking with little chance of success and moving off to search for other prey (Keenleyside 1979). This conflict may not hold for large carnivores, especially tuna. Near reefs predators may shadow prey schools for long periods, awaiting an opportunity to attack a disrupted school (Hobson 1968).

In addition to visually induced schooling and avoidance behaviour, "alarm behaviour" may be initiated by the release of a pheromone from the epidermal cells of an injured conspecific (von Frisch 1938, 1941). The pheromone-induced alarm reaction has been found to occur in a large number of families, including members of the Clupeidae, Engraulidae, Hepsetidae, Ariidae, Gobiesocidae, Exocoetidae, Scorpaenidae, Serranidae, Carangidae, Sparidae, Clinidae, Gobiidae and Scombridae (Pfeiffer 1977). Many of the species in which the substance is absent are either cave-dwelling, predaceous, nocturnal, electric, armoured, solitary or they occur in cryptic habitats. On the other hand, those with pheromones are usually social, lack defensive structures or are generally non-predaceous (Pfeiffer 1977). Presumably the hormone augments visual information on predation or is important in water with restricted visibility such as in turbid water or at night.

Despite these advantages, schooling prey are still successfully taken as has been demonstrated in this study and from experimental work (e.g. Neill & Cullen 1974, Major 1978). One important counter-strategy appears to be schooling by the predators. Predators search for prey using several senses, including scent, sound and vision and the search area scanned by several predators moving parallel is greatly increased, as has been found in pack hunting catfishes (Bruton 1979). Partridge (1982) found that bluefin tuna may search in this way by swimming in forward directed crescents. Aerial photographs also revealed that the parabola is formed by groups of 10 - 20 fish. Similar observations have been made on groups of marine mammals (Martinez & Klinghammer 1970, Norris & Dahl 1980).

Another counter-strategy is attacking at twilight (Hobson 1965, 1968, Collette & Talbot 1972, Major 1977) although tunas feed throughout the day (Magnuson 1969). At dawn and dusk predators appear to be able to see better than the prey partly because of pre-adaptation of the eyes (Olla &

Studholme 1972) and also because of eye pigments which are particularly sensitive to twilight (Muntz & McFarland 1973, Hobson *et al*. 1981).

Schooling by predators and prey appears to be under some degree of internal rhythm (Olla & Studholme 1972 for *P. saltatrix*), becoming more cohesive by day. Kruchinin *et al*. (1981) have described *T. albacares*, *Pneumatophorus japonicus*, *Clupea pallasi* and *Engraulis japonicus* swimming throughout 24 hours, becoming disorganised and slower at night but more active and organised by day.

Predators may use various strategies to overcome defensive schooling. Bluefin tuna herd prey to the centre of the crescent where it is surrounded and consumed (Partridge 1982). Yellowtail appear to herd their prey similarly. Schmitt & Strand (1982) described how seven *S. lalandi* split a large school. The fish were herded by the crescent-shaped school of predators to shallow water after which the yellowtail took turns to penetrate the school, which was surrounded and herded against a subtidal wall. Four charges were witnessed. Yellowtail used a different tactic in attacking Cortez grunts which attempted to escape to the shelter of a reef. In this case the yellowtail cut off the escape route and moved the school into deep water where they continued attacking. The authors speculate that co-operative foraging allows the predators to feed throughout the day and reduces the necessity of crepuscular feeding which has been observed with many fish predators (Hobson 1968, 1972, Major 1977). They maintain that the behaviour is well developed in open-water predators. Observations made on tuna (both *K. pelamis* and *T. albacares*) feeding in the present study suggest that prey (e.g *Sardinops ocellata*) may be herded towards the surface where they are attacked, again indicating co-operative hunting and the use of natural barriers in confining prey.

Predatory attacks by *Caranx ignoblis* on *Stolephorus purpureus* described by Major (1978) suggest that their behaviour has not been developed to such a fine degree of co-operation, which may reflect their opportunistic and often substrate-associated feeding behaviour. In this case the leading predator attacked the school at speed while the following carangids attacked the fragmented school. The leader had the advantage in this situation. Major (1978) noted that individual predators had a better chance of catching a single prey, because of reduced interference.

One aspect not normally considered in schooling behaviour is interspecific co-operation. However, observations made in this study (described for *K. pelamis*) suggest that when several top predators attack a school simultaneously the predators have a greater advantage as their different attack strategies (e.g. plunge-diving gannets, penguins and schooling tuna) confuse and break up the school, making members more vulnerable. This has also been suggested in a tuna-porpoise association (Wolff 1982) in which both animals were found to take very similar prey (Perrin *et al*. 1973, Wolff 1982).

Seasonality of pelagic predators in inshore waters

K. pelamis and *T. albacares* are found in inshore waters from about December to May although it was shown that they occur offshore over a longer period. The other pelagic predators were caught throughout the year and stomach contents were collected from inshore waters in each of the bi-monthly periods. This, however, needs confirmation from analyses of catch and effort data as there is also a decrease in effort over winter when inclement weather reduces angling (pers.obs.). Both *L. amia* and *P. saltatrix* are known to migrate to Natal to spawn (van der Elst 1976, 1981 and pers.comm.) in spring. However, either the migration is asynchronous or part of the population remains in the eastern Cape, accounting for their capture throughout the year. Similarly *A. aequidens* and *S. lalandi* appear to move through eastern Cape waters, becoming sporadically abundant. The causes and precise timing of their movements have yet to be established. It nevertheless appears that pelagic predators are most common in Algoa Bay and adjacent inshore waters from about December to May, thereafter becoming relatively scarce. This is probably governed by intrinsic breeding rhythms and extrinsic factors such as the abundance of prey.

Seasonal and annual trends in pelagic prey

Examination of seasonal variations of prey taken by pelagic predators, revealed that *S. ocellata* and *E. capensis* are important prey in the first half of the year, but decrease thereafter. This suggests that these species move out of shallow coastal waters in winter. There are variations in other prey, for example *L. reynaudi*, which may also move inshore and offshore seasonally. Some of the variations may also reflect changes in relative abundance of several other prey species which may have a masking effect.

Annual variations in principal prey also showed large fluctuations between predators. It was noted, however, that S. ocellata was particularly abundant in 1978, as was shown in the two tunas, while pilchards appeared to be less abundant in 1979. This was also found by Batchelor (1982) working on the diet of gannets in Algoa Bay during the same period. Another general trend is the apparent increase in abundance of Engraulis capensis from 1978 to 1980. From these results it appears likely that predatory fishes can provide insight into the relative abundance of their prey.

Other Pelagic predators

Teleosts

In addition to the six species of pelagic predators described above, three others were encountered during this study: Sarda sarda (Bloch, 1793), Thrysites atun (Euphrasen, 1791), Arygrozona arygrozona (Valenciennes, 1830). They occur in coastal waters, while the latter two are usually caught offshore.

S. sarda preys principally on S. ocellata and E. capensis and T. atun or T. trachurus and S. japonicus (Table 17). Prey differences are possibly the result of the small samples, 20 and 16 respectively. Nepgen (1982) found that T. atun feeds principally on E. capensis and S. ocellata in False Bay while T. trachurus is taken relatively seldom (1%F, N=1068). In addition, 11 species of fish, 3 crustacean taxa and L. reynaudi were found. Nepgen (1979) suggested that T. atun feeds in a density-dependent manner on the most available prey and found that the commonest component of the trawl fishery in a particular year was also the commonest prey of snoek. Furthermore, he noted that trawled T. atun took different prey - lantern fish, hake and euphausids, which suggests that hand-lined specimens may be biased towards pelagic prey.

A. argyrozona, a member of the Sparidae, appears to feed largely on pelagic prey. Nepgen (1977) records more demersal prey, possibly because he had a larger sample (100). For the purposes of this study the pelagic prey suggest that A. argyrozona should be grouped with other pelagic predators, although more information is needed. The body shape and feeding habits suggest convergent evolution with other water column foragers (Davis & Birdsong 1973).

Table 17. The prey of 3 pelagic teleost predators forwhich limited data were collected in this study. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

	Sarda sarda			*Thrysites atun*			*Argyrozona argyrozona*		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M
Polychaeta							7.1	4.8	0.7
CRUSTACEA									
Mysidacea							7.1	14.3	0.5
Megalopa larvae							7.1	9.5	0.1
MOLLUSCA									
Loligo reynaudi				6.3	4.3	0.1	21.4	14.3	4.6
Ommastrephidae							7.1	4.8	21.4
Octopoda							7.1	4.8	1.0
OSTEICHTHYES									
Unidentified fish	25.0	20.6	4.0	12.5	8.7	2.3	14.3	9.5	1.7
Etrumeus teres	5.0	1.7	2.2	25.0	21.7	7.8			
Sardinop ocellata	80.0	57.0	64.0	6.3	4.3	1.9	7.1	4.8	16.7
Engraulis capensis	35.0	19.0	29.5	25.0	39.1	12.1	28.6	28.6	46.0
Trachurus trachurus	5.0	1.7	0.2	25.0	17.4	60.1			
Scomber japonicus				6.3	4.3	15.7	7.1	4.8	7.4
Totals	20	58	218.9	16	23	1321.0	14	21	107.7

Scomber japonicus is also piscivorous when adult, although no samples were collected in this study. Baird (1978b) found that *Lampanyctodes hectoris* was the most common prey in fish taken between Lamberts Bay and Cape Agulhas. Nepgen (1982) reported that *S. japonicus* of 280 - 490 mm took *Engraulis capensis, T. trachurus*, copepods and Brachyura during a survey of the prey of False Bay fishes. A similar pattern is likely to occur off the eastern Cape.

Elasmobranchs

Knowledge on the feeding of sharks is very limited in South Africa because most information to date has been collected incidentally during taxonomic surveys of the fauna (Bass *et al*. 1973, 1975a,b,c,d, 1976). Of the sharks that occur in the eastern Cape *Carcharhinus brachyurus* (Günther, 1870), *Carcharhinus obscurus* (Lesueur, 1818), *Sphyrna zygaena* (Linnaeus, 1758), *Isurus oxyrinchus* (Rafinesque, 1810), and *Galeorhinus galeus* (Linnaeus, 1758) are most likely to have prey common to the other pelagic predators (Bass *et al*. 1973, 1975b, 1975c, van der Elst 1979 and pers.obs.). However, the extent of the overlap and details of this predation will only be resolved by intensive research.

Birds

Gannets (*Sula capensis*) are important predators of pelagic fish, especially *S. ocellata* and *E. capensis* (Batchelor 1982). Similarly penguins (*Spheniscus demersus)* also prey on pelagic schooling fish and squid in the eastern Cape (Randall *et al*. 1981). The large breeding colonies of these species in Algoa Bay suggest that they must have a considerable impact on pelagic prey resources.

Marine mammals

The common dolphin (*Delphinus delphis* Linnaeus, 1758) is frequently found in inshore waters of the Cape and Natal (Ross 1979, Cockroft & Ross 1983). Their prey is exclusively pelagic fish. *S. ocellata* is the dominant prey, at least in Natal. More limited data from the eastern Cape suggest a similar trend there (Ross 1979), indicating that the common dolphin has a food resource overlap with pelagic teleosts.

Principal pelagic prey

This study has revealed interesting new information on the length composition and easterly distribution of several pelagic prey.

Information collected on Sardinops ocellata, Engraulis capensis, Etrumeus teres, Scomberesox saurus, Scomber japonicus and Loligo reynaudi taken by all the teleost predators examined in this study will be synthesized and discussed in relation to the literature. Inshore (<8 km south of Cape Recife), and offshore (>8 km south of Cape Recife) material is compared to reveal areal differences in the length distribution of prey.

Sardinops ocellata

Plots of total length frequencies of S. ocellata collected from all the teleost predators were grouped for bimonthly periods for all years (Fig. 30). Annual plots for the three principal sampling years, for which most data are available, are also shown.

The histograms show that recruitment appears to occur in November-December but probably occurs over a longer period because peak spawning is from September to February, at least in the western Cape (Davies 1956a). Pilchard eggs were found in the plankton throughout the year by Davies (1956a). In South West African waters similar peaks were found in August-September and a lower one in February-March (Mathews 1964) although regional differences have been reported by King (1977). Anders (1975) has reported pilchard eggs off the east coast between the Bashee River and Algoa Bay in late winter with a peak egg collection in August 1973.

In addition to material gathered from predator stomachs contents, opportunistic samples of fresh S. ocellata were collected as follows:

1978.11.04	Part of a school of late-larvae/early juvenile S. ocellata measuring between 28 and 35 mm TL were dipnetted from Port Elizabeth harbour.
1979.05.27	Part of a school of S. ocellata between 159 and 239 mm TL were obtained by throw-netting from a ski-boat in Algoa Bay.
1979.11.30	A sample of pilchards of 138 - 234 mm TL was collected from a ship doing a survey for squid in Algoa Bay.
1981.10.19	Part of a school caught in a large tidal swimming pool in McArthur Bath, Algoa Bay, was sampled and found to be made up of fish between 49 and 77 mm TL.
1982.09.29	Part of a school of S. ocellata (45 - 60 mm TL) was stranded next to McArthur Bath, Algoa Bay.

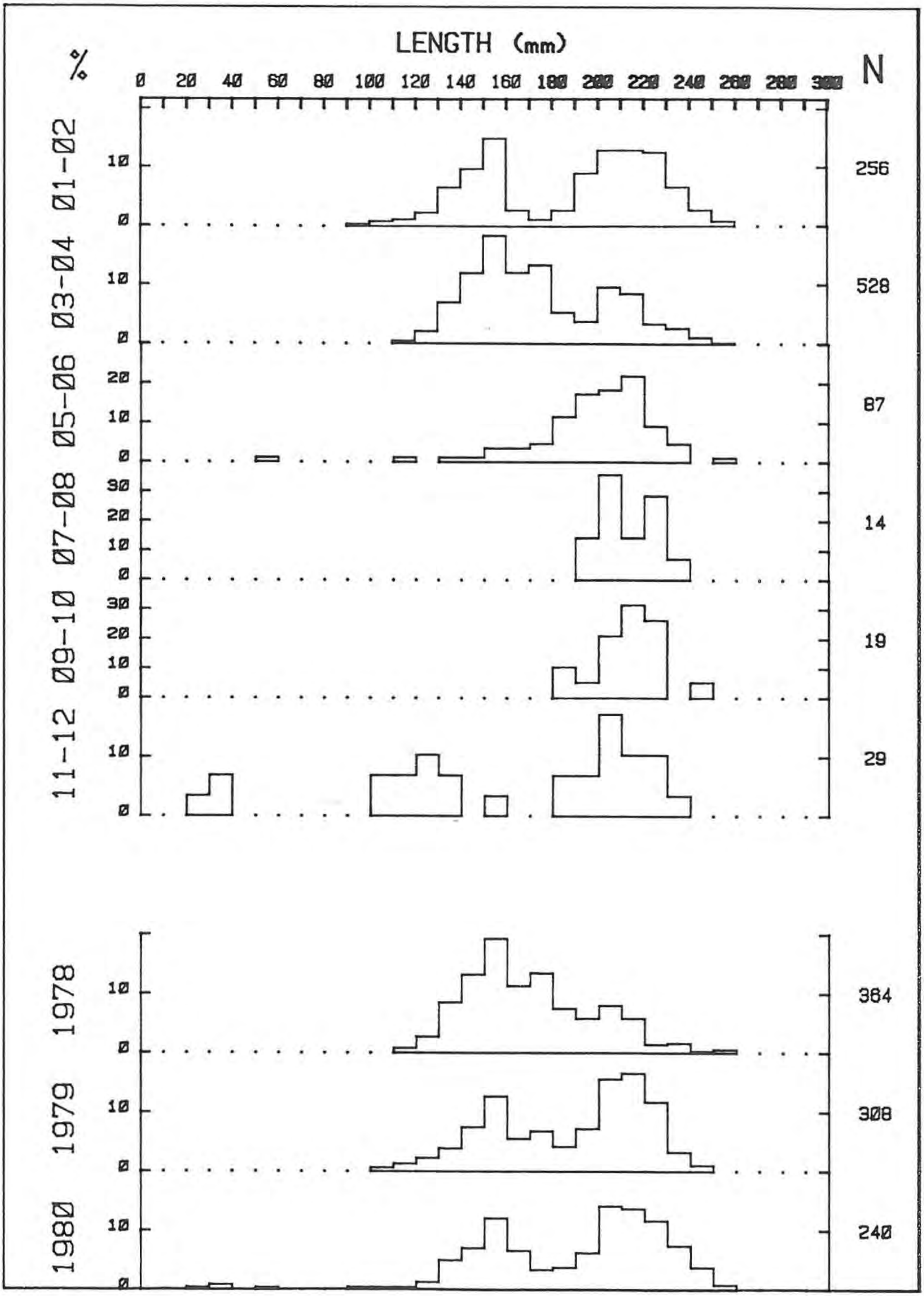


Fig. 30. Bi-monthly (all years combined) and annual histograms of Sardinops ocellata (TL) taken by all predators.

The length distribution of S. ocellata taken in the three years of most intensive sampling is shown in Fig. 30. For each year length compositions are generally consistent and modes probably represent year classes.

There is some difficulty in transforming length data of fish to age classes because of differential growth rates of cohort members giving rise to age groups overlapping in size (Crawford et al. 1978). By converting total lengths used here to standard lengths used by Crawford et al. (1978), it appears that pilchards of 0 years (25 mm TL) to about four years (approx. 249 mm TL) were recorded from stomach contents. The majority were probably one-year-olds (about 150 mm TL) to three-year olds (about 200 mm TL). The two-year-old peak is probably 170 - 180 mm TL but is not clearly defined in these figures. To clarify these preliminary age estimates the otolith material collected during this study should be aged to give a clearer insight into the pilchard population in the eastern Cape.

The length range of S. ocellata recorded by Batchelor (1982) from a breeding colony of gannets on Bird Island, Algoa Bay, during 1978 to 1981 conformed fairly well to that of larger pilchards recorded in this study. They ranged between 65 and 240 mm TL, the majority measuring 154 to 234 mm TL. The annual modes recorded by Batchelor (1982) also correspond with modes recorded here. However more small pilchards were recorded during this study because a wide size and species spectrum of fishes was monitored. Gannets, on the other hand, show a preference for large fish.

Comparing the range and modes of the annual sardine run in Natal (van der Byl 1979a,b, 1980) suggests that only the large size groups occur (or at least are netted or stranded) in Natal.
The range and modes recorded were:
1978 : range: 174 - 235 mm TL. mode: 198 - 204 mm TL.
1979 : range: 186 - 241 mm TL. mode: 211 - 217 mm TL.
1980 : range: 160 - 247 mm TL. modes 180 - 186 mm and 223 - 229 mm TL.

Brownell (1979) recorded that S. occellata eggs are rare in inshore waters, suggesting that they may have an offshore distribution. However, judging by the length distribution of 25-255 mm inshore compared to 124-252 mm offshore, it appears that juveniles may prefer inshore waters (Fig. 34).

Crawford (1981a) suggested that two-year old fish move from the Cape Agulhas region and are responsible for the Natal 'sardine' run each winter when schools have been reported moving through Transkei waters to Natal where they may strand (Davies 1956b, Baird 1971, Heydorn _et_ _al_. 1978, van der Byl 1979a,b, 1980). This study showed that _S. ocellata_ were taken off East London in mid-year, confirming this seasonal migration. However, spawning grounds have been found off the east coast (Anders 1975) and the results of the present study suggest that 0+ to four-year-old fish occur in the eastern Cape throughout the year. Observations made during this study suggest that these fish move inshore in summer when they enter bays. In winter they appear to move offshore and up to Natal where they are preyed on by demersal and pelagic fishes and birds (Hecht 1976, Batchelor 1982, this study). The situation is therefore considerably more complex than was initially believed and comprises more than a simple migration from the south coast (Davies 1956b, du Plessis 1959). This stock may partially account for the large population increase of gannets on Bird Island, Algoa Bay (Randall & Ross 1979). The impact that bird predators may have on a fish population has recently been described by Furness & Cooper (1982) who estimated that three seabird species take approximately 30% of the commercial mean annual catch in the Saldanha Bay fishing ground.

Crawford & Shelton (1978) have attributed the decline of seabird breeding populations on the west coast to overfishing by commercial trawlers. Overfishing resulted in the reduction of peak catches of 410 159 metric tons in 1962 to 104 153 metric tons in 1972 and 46 200 metric tons in 1981 (Crawford 1981a and Crawford pers.comm.). This decline has been observed despite extensive management-oriented research (e.g. du Plessis 1959, Davies 1956a,b, Newman 1970a,b, Crawford 1981a) and some catch restrictions. On the one hand the catch restrictions appear to need improvement and on the other, more work on predator-prey studies is necessary to improve prediction models and assist in fisheries management.

Engraulis capensis

E. capensis is a principal prey species of pelagic predators. An analysis of the total length frequencies of anchovy taken by all predators for all years combined is shown in Fig.31. A range from 21-163

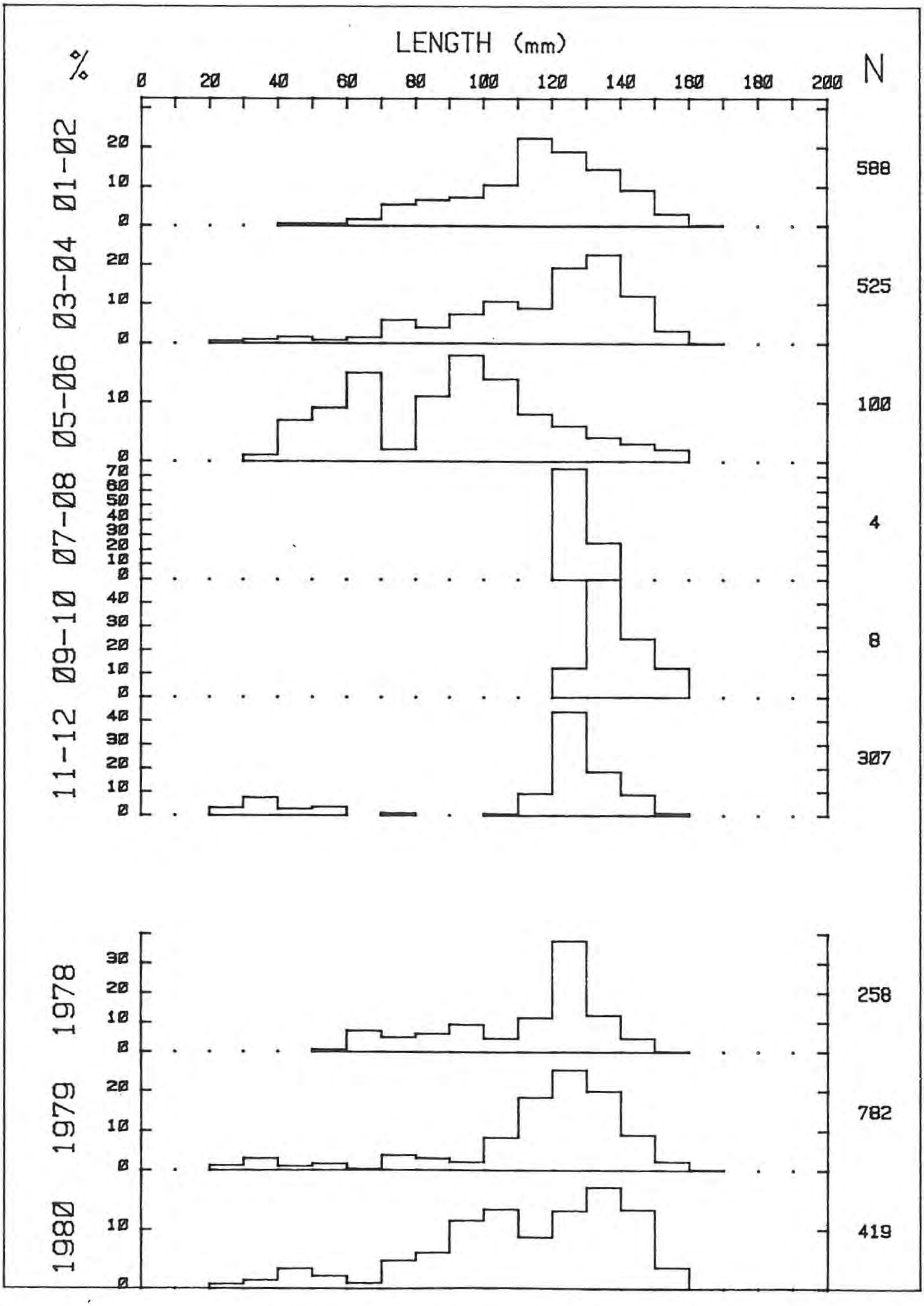


Fig. 31. Bi-monthly (all years combined) and annual histograms of *Engraulis capensis* (TL) taken by all predators.

mm was recorded from predators' stomach contents. According to length-age data (Crawford et al. 1978), the anchovy obtained from piscivorous fish were between 0-3 or 4 year old. Evidence of juvenile recruitment into the population was found from November to April. These fish were taken from predators, especially P. saltatrix and L. amia caught close inshore in Algoa Bay, between the harbour breakwall and the St Croix group of islands. Their range is, however, more extensive.

Anders (1975) reported anchovy eggs on the South African east coast between the Bashee River and Algoa Bay. Larvae have subsequently been found in very high numbers in Algoa Bay and these formed 35.1% of the ichthyoplankton off sandy beaches (Beckley, University of Port Elizabeth, pers.comm.) Anchovy taken inshore in the present programme measured 21 - 163 mm compared to 71 - 152 mm offshore (Fig. 34), suggesting a spatial segregation of small juveniles inshore. Larvae and juveniles are also important prey of terns (Sterna spp.) (pers.obs., Randall & Randall 1978). Gannets take large anchovy (67 - 174 mm TL) predominantly, suggesting that they select the largest anchovy available (Batchelor 1982). Considering the importance of anchovy in gannet diets on Bird Island, it is likely that they have had a substantial effect on the population increase of gannets on the island (Randall & Ross 1979).

An outstanding feature of the anchovy taken by predators was that large adult fish were often taken, compared to 0-year-old fish caught in the western Cape trawl fishery, which contributed about 50 - 80% of the catch from 1966 to 1976 and which reflects the heavy exploitation (Crawford 1981b). Commercial anchovy fishing was recorded in the western Cape in 1958 but this species began dominating the catch in 1967 and made up 87.3% of the combined purse seine catch by 1974. Annual catches are currently running between 209 500 and 315 500 metric tons for the period 1978 to 1981 (Crawford 1981b & pers.comm.).

The anchovy fishery is potentially very unstable because of the species' short life span, the dependence on 0-year-old fish in the commercial fishery and the possiblity of a weak cohort due to unfavourable environmental conditions. The eastern Cape portion of the anchovy population may make a positive contribution by buffering such fluctuations with its large and relatively more stable age structure, and contributing juveniles to the western Cape population. This clearly needs further research.

Etrumeus teres

E.teres is an important prey of tuna. Juveniles were found inshore during summer, and were taken by Cheimerius nufar and Pomatomus saltatrix. The total length frequency of E. teres recovered from all predators' stomachs in bi-monthly periods and in 1978 to 1980 is given in Fig. 32.

Analysis of the material collected from 1978 to 1980 is presented in Fig. 32. Similar peaks suggest they may be made up of different age classes. The range of 62 to 238 mm total length is probably made up of 0 to 4 or possibly 5-year-old fish, using the length-age data of Crawford et al. (1978). Recruitment of juveniles in the eastern Cape occurs from November-December to March-April (Fig. 32), when they are often found inshore, and are taken by small piscivores. Beckley (pers. comm.) has recorded larvae and early juveniles in Algoa Bay. The clupeids, which were made up largely of E. teres, comprised 23.5% of the total numbers sampled in 1980 to 1982. The modal peaks conform with age classes according to the data of Crawford et al. (1978). For example, in January-February the modal midpoints of 85, 125, 185 and 235 mm TL would be composed of fish of 0, 1, 2 and 3 or 4y fish. However, otoliths should be read to confirm these estimates, especially as these fishes are living in water which is warmer than on the west coast.

The apparent shift in size(=age) composition between 1978 and 1980 is probably a sampling bias caused by disproportionate sampling of inshore fish, which feed largely on juvenile round-herring, and offshore fish, which take large specimens. The length range is roughly equivalent over this period which would be a better reflection of the population size structure. It appears that E. teres is found throughout the year in the eastern Cape.

Crawford (1981c) found from aerial sightings that E. teres usually occurs more than 15 km offshore and noted the age composition recorded in the commercial fishery, which is largely made up of 0-year-old fish, is caused by the preference of skippers to fish close inshore. This

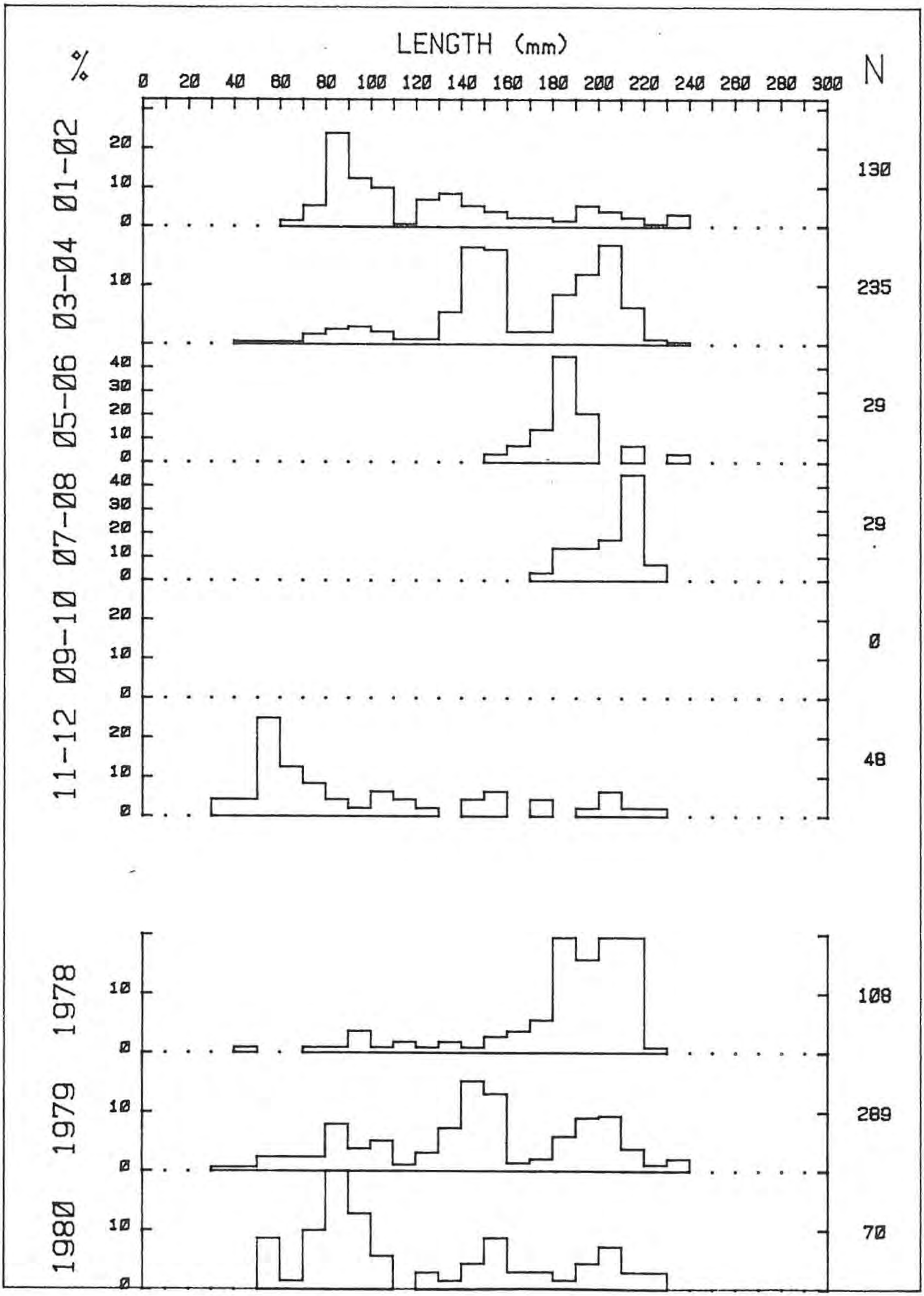


Fig. 32. Bi-monthly (all years combined) and annual histograms of *Etrumeus teres* (TL) taken by all predators.

suggestion is confirmed in Fig. 34. The length distribution of E. teres inshore was 33 - 208 mm TL compared to 156 - 238 mm TL offshore, showing a clear separation of size classes. Fish up to 2 years of age occur inshore, those more than about 2 years live offshore. Crawford (1981c) believes that 2-year-old fish move offshore, possibly for spawning . The offshore distribution of large fish may account for the infrequency of this prey in the diet of gannets on Bird Island, Algoa Bay (Batchelor 1982), as gannets appear to feed largely inshore (Batchelor 1982, pers.obs.).

Scomberesox saurus

Earlier it was shown that S. saurus was most abundant in the diet of tuna from March to June offshore, and in March-April in Algoa Bay and May-June off East London. Length distributions inshore range from 116 - 315 mm TL (Fig. 34). Offshore sizes ranged between 208 and 460 mm TL (fish larger than 400 mm are not included in Fig. 34), and showed a clear size segregation. Batchelor (1982) found that gannets on Bird Island take S. saurus mainly in the autumn, winter and early summer (March to November). The limited data suggest that S. saurus may be present throughout the year, but more dominant in winter. Clearly more work is necessary before the seasonality and biology of the species in this area is understood.

Scomber japonicus

S. japonicus was taken by pelagic predators. Although important in the western Cape, little is known about its distribution in the eastern Cape. The length range taken in this study was 86 - 329 mm, with juveniles dominating the sample (Fig. 34). Baird (1978a) notes that S. japonicus was first recorded in the western Cape commercial fishery in 1954 and that it has subsequently been found in the catch in fluctuating quantities. In 1954 4 000 metric tons were recorded and in 1975 69 000 metric tons were attributable to this species. Spawning has been recorded from June to September when mature fish move inshore (Baird 1978a). S. japonicus is planktivorous below 250 mm SL, but fish contribute more to the diet with growth and S. japonicus larger than 450 mm SL are largely piscivorous (Baird 1978b). According to the age estimates of Crawford et al. (1978) the fish recorded in predators' stomachs are probably 0 to one-year-olds.

Trachurus trachurus is discussed in Chapter 5. It is preyed on extensively by demersal species.

Loligo reynaudi

The myopsid squid *L. reynaudi* was the single most important cephalopod in the diet of pelagic and demersal fish. The combined length frequencies recorded from all predators in this study are shown in Fig. 33. Neither the bi-monthly nor the annual length groupings show a clear trend. A range of 62-325 mm VML was recorded.

Batchelor (pers.comm.) found that the ventral mantle length distribution of *L. reynaudi* caught by commercial trawlers varied between 83 and 376 mm with one principal and at least two additional modes being present in all months. The principal modes varied between 139 and 146 mm and 174 to 181 mm but in this study they went up to 200 - 220 mm.

Males grow larger than females and reproductive activity is evident in males larger than 83 mm and females larger than 76 mm (Batchelor pers.comm.). Hatanaka *et al*. (in prep) found that 50% maturity was attained at 160 mm and 200 mm DML in females and males respectively. Hatanaka *et al*. (in prep.) noted that individuals within a trawled school have similar length composition although it was strongly correlated with depth. Although no detailed study has been published on the diurnal depth distribution of *L. reynaudi*, Vaughan & Recksiek (1978) have investigated the vertical distribution of *Loligo opalescens* off California using echo traces combined with diving observations, underwater cameras and simultaneous catching. The four types of traces identified resulted from the school formations either close to the bottom or in midwater. Apparently they may be in either position both day and night, probably depending on activities such as breeding and feeding. This is likely to hold too for *L. reynaudi*.

Several loliginid squids lay "fingers" of eggs in aggregations on the bottom. Examples are *L. reynaudi* (Batchelor pers.comm., Hatanaka *et al*. in prep., pers. obs.), *L. forbesi* (Holme 1974), *L. opalescens* (Fields 1965) and *L. pealei* (Griswold & Prezioso 1981). During this stage they are particularly vulnerable to predation by pelagic, benthic and demersal fish such as *Petrus rupestris*, *Epinephelus guaza* and *Cheimerius nufar*. Griswold & Prezioso (1981) described in some detail the pairing and egg laying of *L. pealei* from observations in the wild. Their observations may well apply to *L. reynaudi* as they also record no evidence

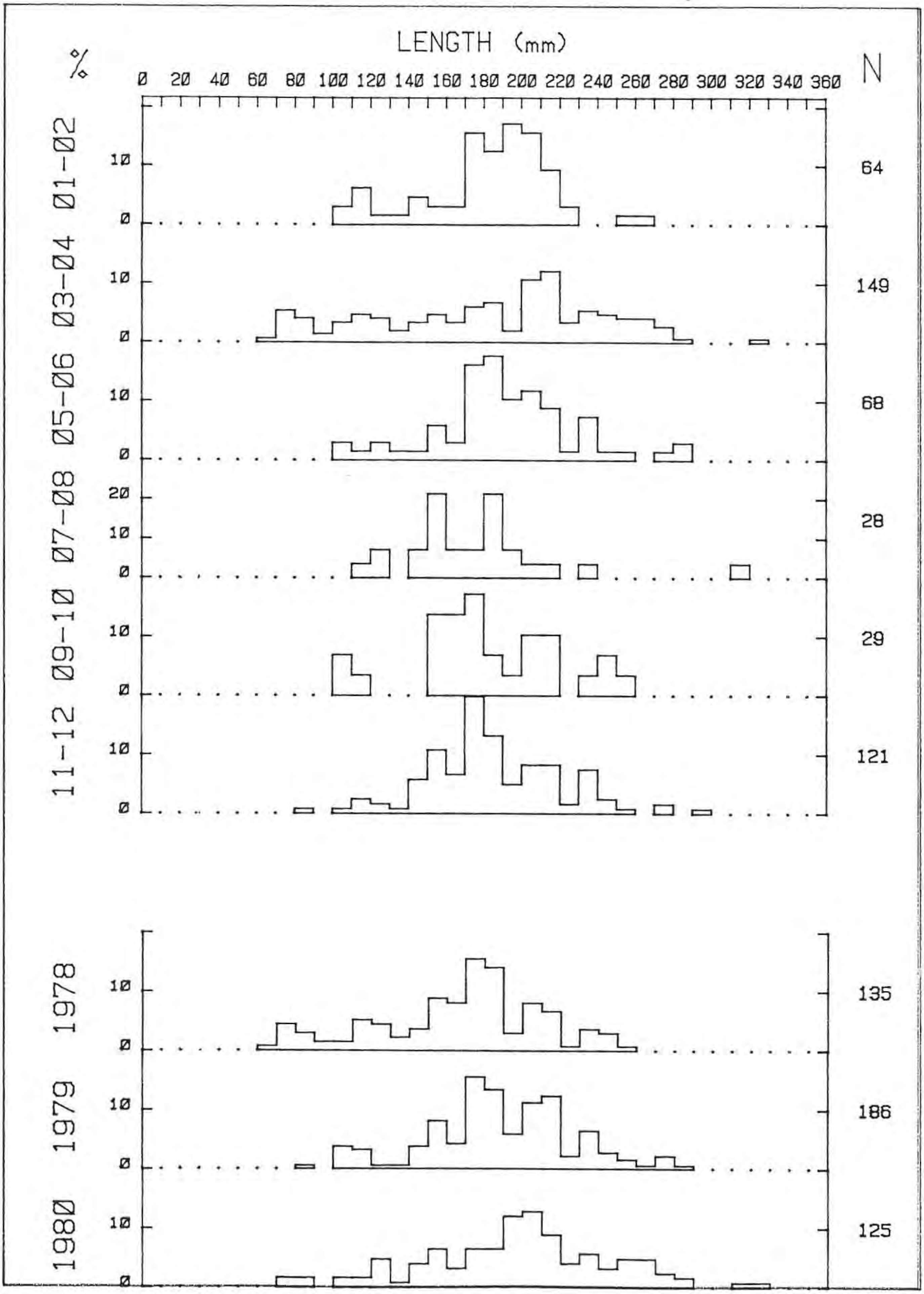


Fig. 33. Bi-monthly and annual histograms of Loligo reynaudi (VML) taken by all predators.

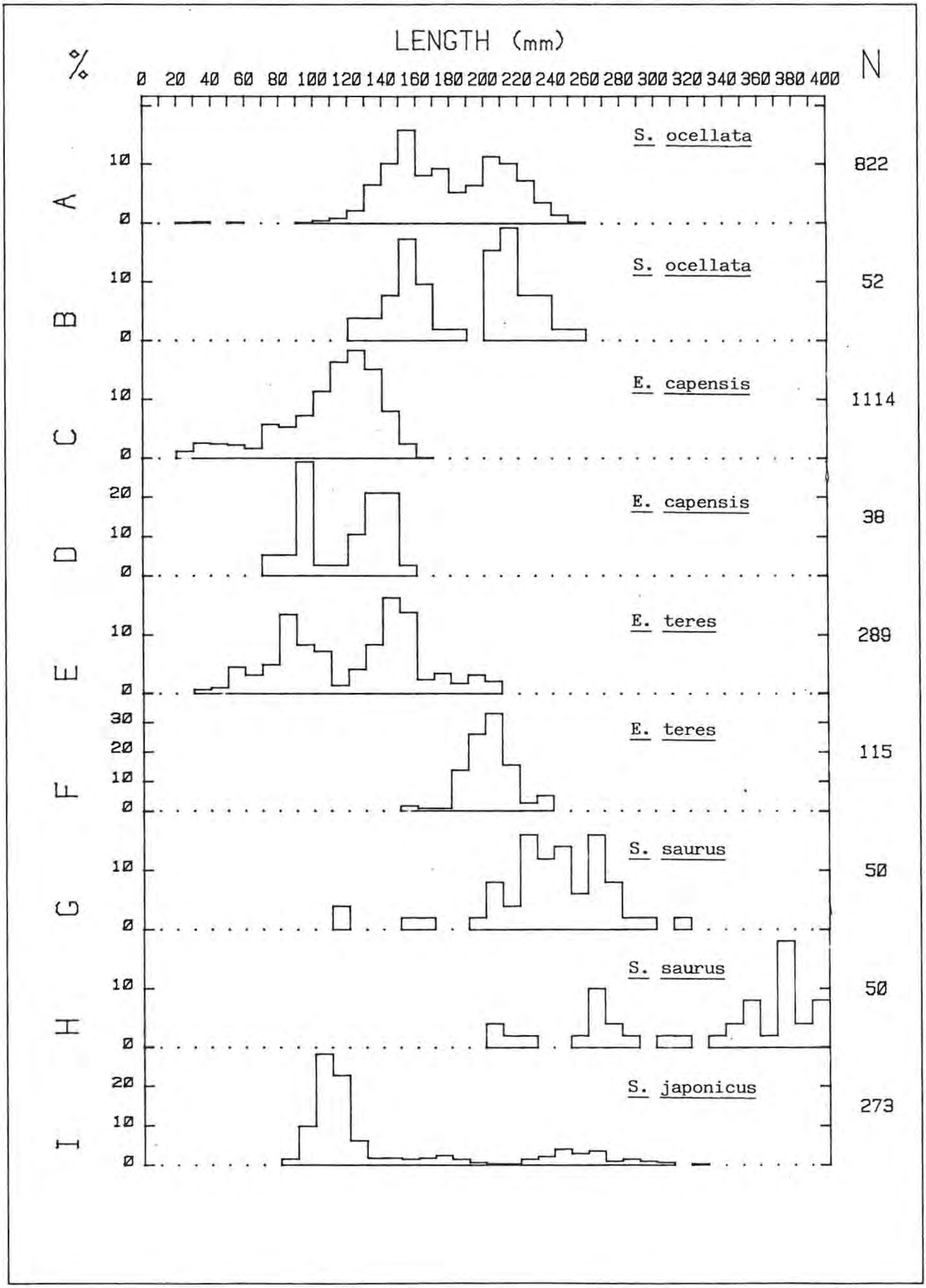


Fig. 34. Histograms of Sardinops ocellata (A,B); Engraulis capensis (C,D); Etrumeus teres (E,F) Scomberesox saurus (G,H) taken inshore (A,C,E,G) and > 8 km south of Cape Recife (B,D,F,H). (I) Histogram of Scomber japonicus taken in all areas.

of damaged or dying individuals after spawning and similar egg clusters are laid. L. reynaudi does not appear to die after spawning (Batchelor pers.comm.) so it is not likely to be taken moribund in vast numbers as happens with L.opalescens (Fields 1965).

Conclusion

A variety of prey species are taken by pelagic predators but clupeid and engraulid fishes and Loligo reynaudi are common and dominant prey in coastal areas of the eastern Cape. The relative abundance of these prey appears to vary with time and this is probably an important factor in prey choice. Observations in the field and a literature survey illustrated the importance of schooling in the defence of pelagic prey. Pelagic predatory teleosts often hunt in schools and this appears to be a tactic to overcome the advantage of schooling by prey.

This study also provided new information from the eastern Cape on the occurence and size distribution of the dominant pelagic prey which are commercially important trawl species in the western Cape. This clearly demonstrates the use of such studies in fisheries research, as will be discussed in more detail in Chapter 8.

CHAPTER 5

A DEMERSAL PREDATOR OF SOFT SUBSTRATES

Introduction

Top predatory teleosts which occur predominantly over soft substrates are represented commonly by one teleost in shallow coastal waters: Argyrosomus hololepidotus. Other predators which share the same demersal prey are included in the discussion of A. hololepidotus, although primarily pelagic predators which also take demersal prey have been described in Chapter 4 and will not be covered. Finally, the common demersal prey are discussed and their food is described from the literature to establish the basis of the food web.

Family: Sciaenidae Argyrosomus hololepidotus (Lacepede, 1802)

Common name: kob

Description

The body is elongate and robust (depth ±22% TL; ±43% with dorsal and pelvics extended Fig. 3). The lateral line is gently curved, ending in the caudal fin. The caudal peduncle is robust, and the caudal fin is truncate to emarginate in adults, but rounded in juveniles. The head is large, approximately 24% TL. The eye is large, 3.7% TL. The terminal mouth is big, the gape is 8-11% TL. The maxilla is long, ending below the eye. The gill rakers are well developed, totalling 12-17. With growth the rakers become less elongate and more stubby. The teeth are strong and conical.

Colouration varies from silver to dark grey dorsally and laterally becoming darker in turbid water. Ventrally they are pale to silver. The fins are dark grey to brown. A row of silver spots may be seen along the lateral line, especially in living individuals, and there is a black scaleless axillary patch. The species attains 73.5 kg (van der Elst 1981) and exceeds 2 m. Wallace (1975) records one specimen of 2.39 m.

Distribution

A. hololepidotus is found south of the equator from the west African coast to Natal, Madagascar, Western Indian Ocean off Kathiawar (Seshappa) and the Australian coast, at least from Brisbane southwards to the Bass Straight (Trewavas 1977), but possibly "All round the (Australian) coast but perhaps not in the North" (Roughley 1951 as quoted by Trewavas 1977).

Habitat

Kob are caught throughout the year in the eastern Cape particularly from November to May, and they are relatively abundant in Natal during winter (Wallace 1975). Juveniles and adults are found in estuaries in Natal and in the Cape (Wallace & van der Elst 1975, Wallace 1975, Winter 1980, Marais & Baird 1980a & b, Kok pers.comm.) Larvae have been recorded in the Swartkops estuary (Melville-Smith & Baird 1980) having been washed in by the tide. Large marine nursery areas have recently been found in the eastern Cape, particularly in the shallows (<15 m) of Algoa Bay (Smale in prep.). Estuaries are marginal nursery areas for this species, which is far more common in the sea from the surf zone of sandy beaches (Lasiak 1982) to about 150 m (Chao & Trewavas 1981). There appears to be a major breeding area in the eastern Cape and Smale (in prep.) suggests that A. hololepidotus migrates from other areas of the coast for this purpose. Kob are common over sandy areas by day (Smale in prep.) but are also found in the lee of reefs and wrecks in large aggregations. They are caught in large numbers in the west, north and east of Algoa Bay. St. Croix, Jaheel and Brenton Islands, and areas near the mouths of the Swartkops and Sundays Rivers are popular fishing sites because of the abundance of kob. They are also caught at Riy Bank and Noordhoek more sporadically. Small fish up to about 500 mm occur in large schools. Larger individuals are found in small packs or individually.

Material

A total of 6323 A. hololepidotus was examined, with 509 stomach contents intact. The length frequencies of material examined are presented in Fig. 35. Kob ranged from 226-1701 mm and stomachs were collected from kob ranging from 256 - 1701 mm. Seven large kob collected during an

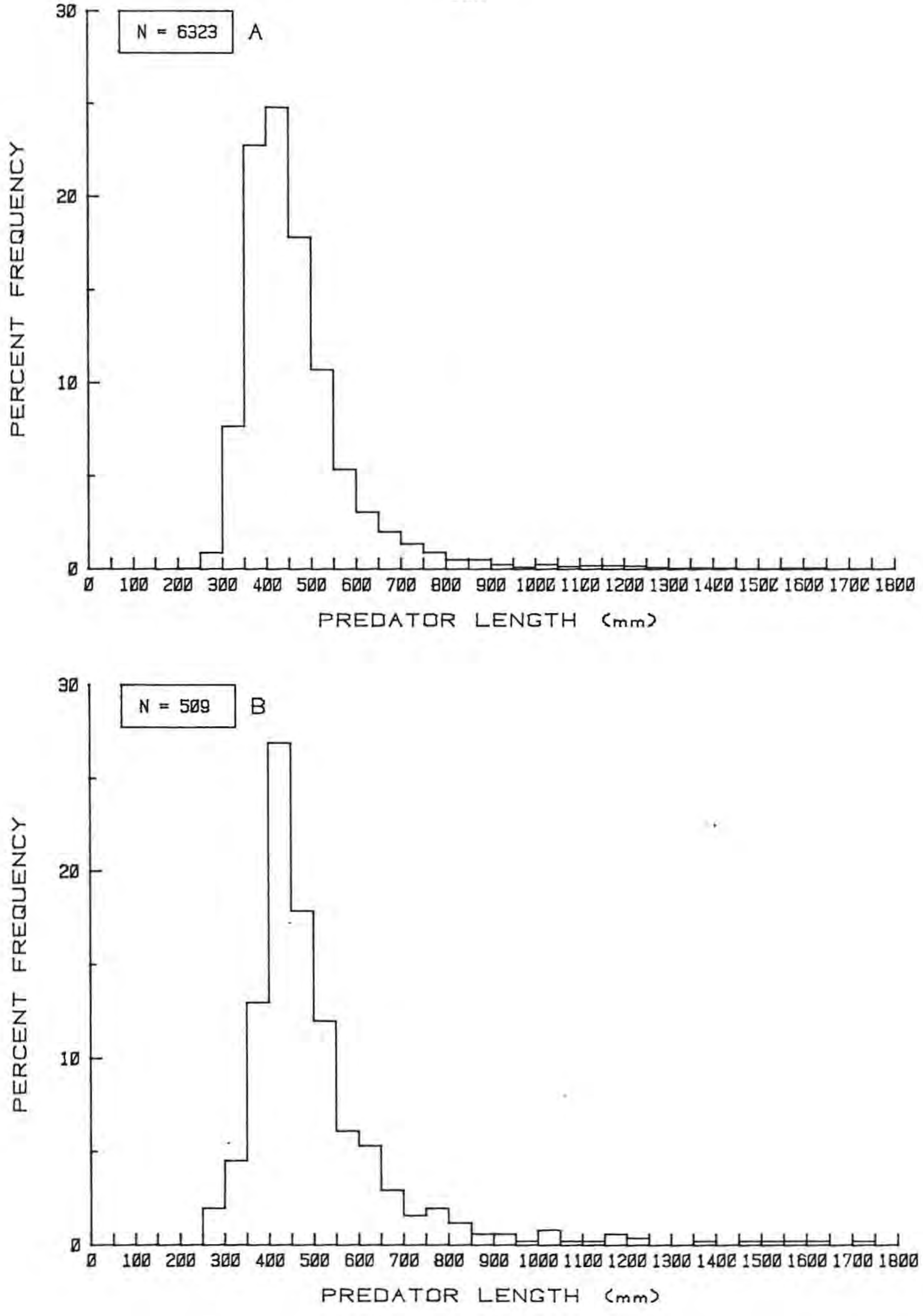


Fig. 35. Histograms of the entire sample of *Argyrosomus hololepidotus* (A) and those containing stomach contents (B).

inshore trawling survey of the eastern Cape (Wallace et al. in prep.; Smale in prep.) were included in this sample with one commercially trawled specimen. The prey species spectrum was the same as recorded in line-caught kob so the data have been combined in the following analyses. The balance of the material was collected by line fishermen who used a variety of baits. They were situated geographically from East London to Mossel Bay although the bulk of the material was collected from Algoa Bay. Most of the fish (92%) had either been gutted or had empty or everted stomachs which result from stress and pressure reduction during capture causing the expansion of the swimbladder. The problem was accentuated beyond 20 - 30 m, consequently the material mainly reflects feeding in shallow (<30 m) marine areas. The maximum stomach fullness recorded was 8.6% of body mass. The highest reconstituted stomach mass was 65% of body mass, which resulted from retention of squid beaks in the stomach.

Feeding

The prey of A. hololepidotus are presented according to size in Table 18 and the principal prey are shown in Fig. 36. The prey of kob of 200 - 300 mm consisted principally of crustaceans (99.7% by number, 89% by mass) and Mysidacea were the most important prey group. Demersal fishes (Ammodytes capensis, Pomadasys olivaceum and Gobiidae) and unidentified fish remains made up the balance (0.4%N, 11%M).

Kob of 301 - 500 mm took a wide variety of prey (41 taxa), which was in part a result of the large number of fish in this group (319). Crustaceans made up 99% of the number and 14% of the mass of prey taken. Cephalopods were not important by number (0.1%) but were important by mass (22%). Of the cephalopods, Loligo reynaudi was the single most important species (11%F, 0.1%N, 20%M). Fishes made up 1% of the number and 64% of the mass of prey. Pelagic schooling teleosts such as Etrumeus teres and Sardinops ocellata made up 0.1% of the number and 14% of the mass of prey taken. Demersal species, especially those associated with soft sediments, dominated the teleosts (1%N, 47%M). Cynoglossus capensis, Argyrosomus hololepidotus and Pomadasys olivaceam were particularly important.

A. hololepidotus of 501 - 1000 mm took 29 categories of prey. Crustaceans accounted for 91% by number and 1% by mass. Mysids were again

Table 18. The prey of *Argyrosomus hololepidotus*, according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

	200 - 300 mm			301 - 500 mm			501 - 1000 mm			1000 - 1800 mm			200 - 1800 mm		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA															
Unidentified crustaceans	10.0	0.1	2.8	1.6	<0.1	0.1							1.2	<0.1	<0.1
Copepoda				0.6	<0.1	<0.1							0.4	<0.1	<0.1
Mysidacea	50.0	99.4	76.9	25.7	98.4	11.8	4.9	90.3	0.6				18.7	97.5	3.4
Caridea				0.3	<0.1	<0.1							0.2	<0.1	<0.1
Penaeidea	30.0	0.2	9.2	8.8	0.1	0.9	7.3	0.5	0.2				8.4	0.2	0.3
Brachyura				0.6	<0.1	0.1				6.3	2.1	<0.1	0.6	<0.1	<0.1
Megalopa larvae				1.3	<0.1	<0.1	0.6	0.1	<0.1				1.0	<0.1	<0.1
Anomura				2.5	0.1	1.0							1.6	<0.1	0.3
Callianassa sp.				0.9	<0.1	0.2							0.6	<0.1	<0.1
MOLLUSCA															
Sepiidae				1.6	<0.1	0.5				6.3	2.1	<0.1	1.2	<0.1	0.1
Lolicinidae				0.3	<0.1	<0.1							0.2	<0.1	<0.1
Loligo reynaudi				11.3	0.1	20.0	22.0	1.0	33.4	31.3	12.7	24.9	15.1	0.2	27.9
Octopoda (Benthic)				0.6	<0.1	0.2							0.4	<0.1	<0.1
Octopus vulgaris				0.3	<0.1	1.4	1.2	<0.1	0.7				0.6	<0.1	0.7
CHONDRICHTHYES															
Unidentified elasmobranch										6.3	2.1	0.9	0.2	<0.1	0.2
OSTEICHTHYES															
Unidentified fish	20.0	0.1	1.7	8.8	<0.1	3.1	10.4	0.5	1.1				9.2	0.1	1.3
Etrumeus teres				1.6	<0.1	1.0	1.8	0.1	0.2	6.3	2.1	0.9	1.8	<0.1	0.6
Sardinops ocellata				3.8	<0.1	4.6	4.3	0.2	4.7	6.3	2.1	1.4	3.9	0.1	3.9
Engraulidae				0.3	<0.1	<0.1							0.2	<0.1	<0.1
Engraulis capensis				5.6	0.1	4.3	2.4	0.2	0.8				4.3	<0.1	1.5
Galeichthys feliceps				10.0	0.4	4.8	14.0	3.5	1.7				10.8	0.7	2.1
Bregmaceros sp.				1.6	<0.1	0.1	0.6	0.2	<0.1				1.2	0.1	<0.1
Merluccius capensis				0.3	<0.1	<0.1	0.6	<0.1	0.5	6.3	8.5	5.8	0.6	<0.1	1.7
Bothidae				0.3	<0.1	0.5							0.2	<0.1	0.1
Soleidae				0.3	<0.1	<0.1							0.2	<0.1	<0.1
Austroglossus pectoralis							0.6	<0.1	0.9				0.2	<0.1	0.5
Cynoglosidae				1.3	<0.1	0.2	0.6	<0.1	0.1				1.0	<0.1	0.1
Cynoglossus capensis				10.3	0.1	12.0	7.9	0.4	4.2	6.3	2.1	0.3	9.2	0.2	5.2
Cynoglossus zanzibarensis				2.5	<0.1	2.4							1.6	<0.1	0.6
Ammodytes capensis	10.0	0.1	1.1	0.3	<0.1	<0.1	0.6	<0.1	0.2				0.6	<0.1	0.1
Cheilodactylus pixi				0.6	<0.1	0.2	0.6	<0.1	0.2				0.6	<0.1	0.1
Chirodactylus brachydactylus				0.3	<0.1	<0.1							0.2	<0.1	<0.1
Acanthistius sebastoides							1.2	<0.1	0.7	6.3	2.1	2.1	0.6	<0.1	0.9
Trachurus trachurus				1.9	<0.1	2.0	0.6	<0.1	1.3	6.3	2.1	4.8	1.6	<0.1	2.3
Pomatomus saltatrix				0.6	<0.1	1.0	0.6	<0.1	0.6	12.5	4.3	6.4	1.0	<0.1	2.2
Scombrops dubius							0.6	<0.1	0.8				0.2	<0.1	0.4
Argyrosomus hololepidotus				15.0	0.2	16.5	22.0	1.2	18.8	25.0	10.6	12.0	17.3	0.3	16.5
Umbrina canariensis				0.3	<0.1	1.3	0.6	<0.1	0.1				0.4	<0.1	0.4
Pomadasys olivaceum	10.0	0.1	6.6	8.5	0.1	7.0	23.8	1.1	20.6	18.8	12.8	2.4	13.8	0.2	12.6
Rhonciscus striatus				0.3	<0.1	0.2							0.2	<0.1	<0.1
Lithognathus mormyrus										6.3	17.0	9.3	0.2	<0.1	2.3
Pagellus natalensis				0.3	<0.1	<0.1	1.2	0.1	2.6				0.6	<0.1	1.3
Rhabdosargus holubi							0.6	<0.1	0.5				0.2	<0.1	0.2
Sarpa salpa							0.6	0.1	0.4				0.2	<0.1	0.2
Scomber japonicus				0.3	<0.1	0.6	2.4	0.1	4.0	18.8	17.0	28.8	1.6	<0.1	9.3
Atherina breviceps				0.3	<0.1	0.6							0.2	<0.1	0.1
Gobiidae	10.0	0.1	1.7	1.3	<0.1	0.1							1.0	<0.1	<0.1
Chelidonichthys queketti							0.6	<0.1	0.1				0.2	<0.1	0.1
Chatrabus melanurus				0.3	<0.1	1.3							0.2	<0.1	0.3
Totals	10	1801	18.1	319	35623	2376.0	164	4167	4653.7	16	47	2353.5	509	41638	9401.3

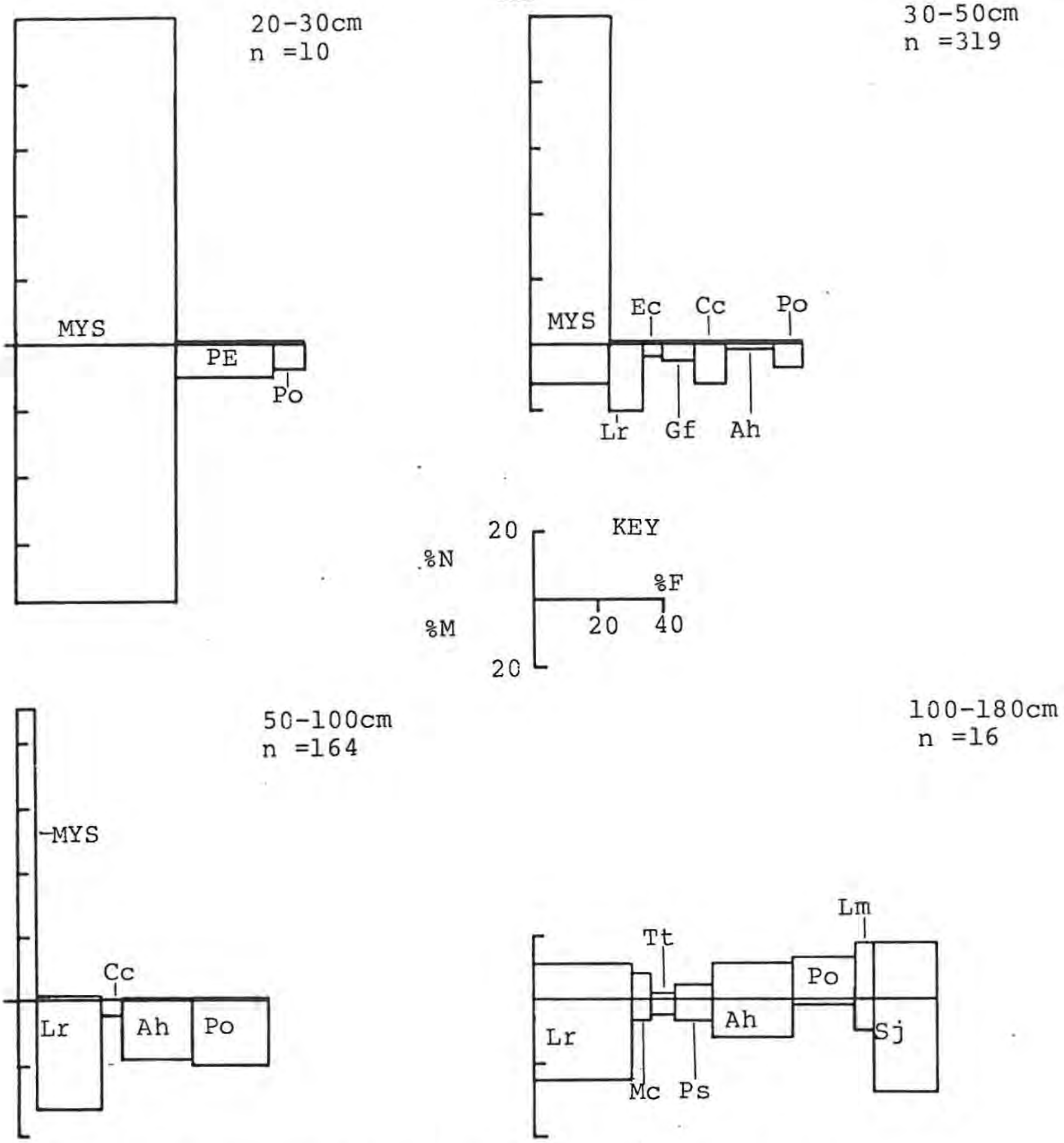


Fig. 36. The principal prey of Argyrosomus hololepidotus.

Ah:Argyrosomus hololepidotus Cc:Cynoglossus capensis Ec:Engraulis capensis
Gf:Galeichthys feliceps Lm:Lythognathus mormyrus Lr:Loligo reynaudi
Mc:Merluccius capensis MYS:Mysidacea PE:Penaeidea Po:Pomadasys olivaceum
Ps:Pomatomus saltatrix Sj:Scomber japonicus Tt:Trachurus trachurus

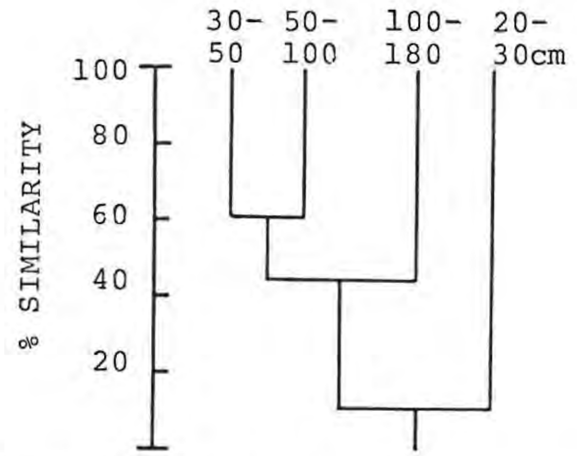


Fig. 37. Similarity dendrograms of diets of Argyrosomus hololepidotus size groups, according to prey mass.

the dominant group, and although they were taken far less frequently (5%) and accounted for a small proportion of the prey mass (1%), they occurred in very large numbers (90%N). The largest kob with mysid prey measured 656 mm. Cephalopods were important, comprising 1% of the number and 34% of the mass of prey taken. Loligo reynaudi dominated this group. Fishes made up the balance of the prey, representing 8% of the number and 65% of the mass of prey taken. Pelagic schooling fish made up 1% of the number and 12% of the mass of prey; demersal species, which were largely associated with sandy substrates, make up 7% of the number and 52% of the total mass of prey. Principal teleost prey species were all demersal; C. capensis, A. hololepidotus and P. olivaceum.

Kob larger than 1000 mm took few crustaceans; brachyuran remains occurred in 6% of the stomachs examined and made up 2% by number but <0.1% by mass of the prey. Cephalopods made up 15% of the number and 25% by mass of the prey. L. reynaudi was again the principal cephalopod taken. Fishes made up the bulk of the diet (83%N, 75%M). They were both pelagic (28%N, 42%M) and demersal (53%N, 32%M) species. S. japonicus was a principal prey which dominated other teleosts by mass. Other major prey were A. hololepidotus, L. mormyrus and P. olivaceum. Similarities in these groups are shown in Fig. 37 according to prey mass.

Predator-prey length relationships

The length relationship between A. hololepidotus and all prey is plotted on Fig. 38. A point of inflection at about 500 mm describes a different relationship below this size. The largest ratio recorded was 57%, the smallest 2%. If mysids and other small crustaceans are included the minimum drops to about 1%. A rapid increase of the prey maximum lengths occurs as kob double in length between 250 and 500 mm. The prey lengths show an increment approximately to the power of 10 (26 - 290 mm). The relative prey size taken is greater over this range than with large specimens. Kob larger than 520 mm took prey which were relatively smaller. Beyond this size there was a notable lack of very small prey.

To clarify prey size selection, important prey taken by different size groups of A. hololepidotus are plotted in Figs 39 & 40. Although there is considerable overlap in prey sizes taken by kob of different length

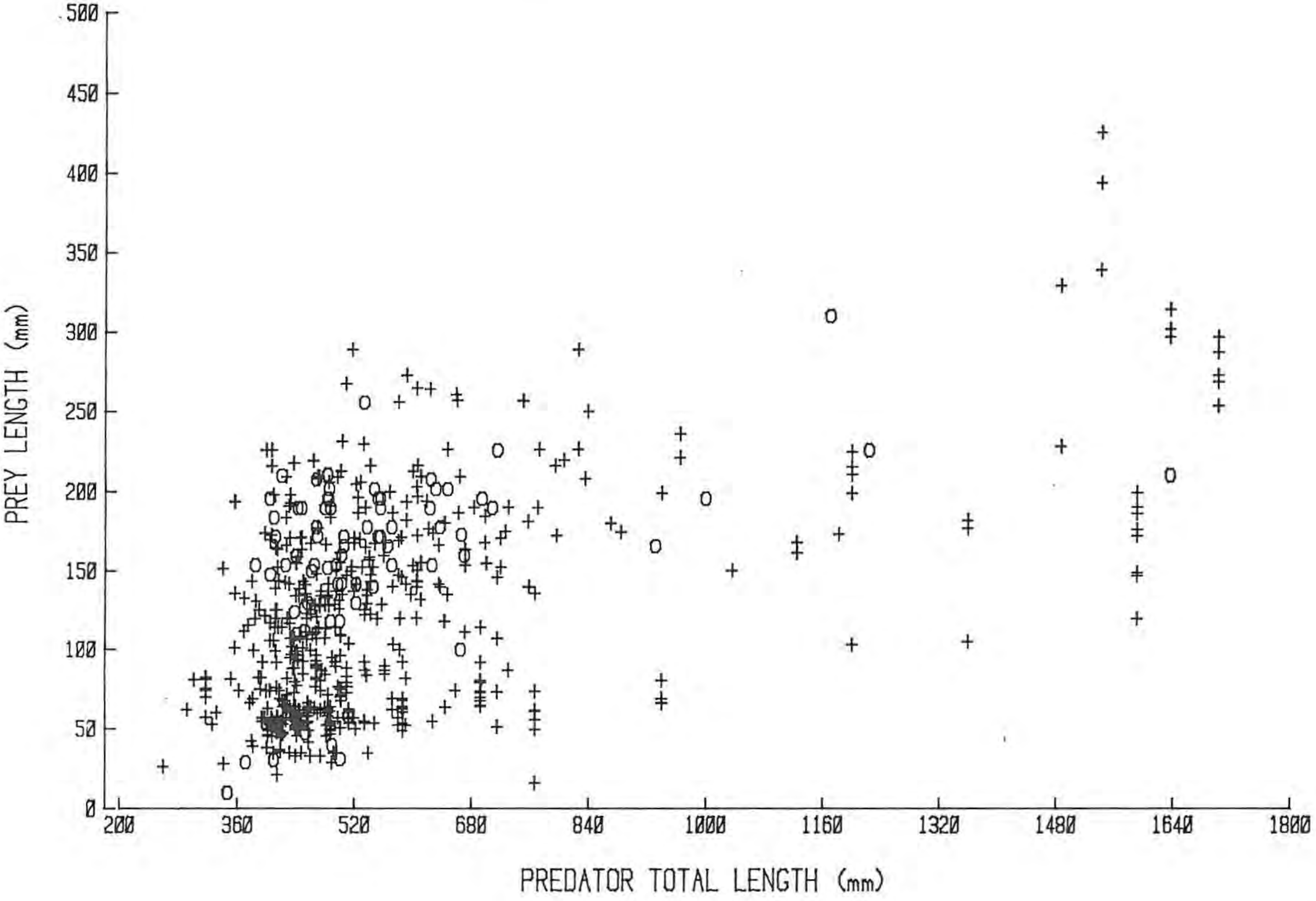


Fig. 38. Scatter diagram of prey length against total length of <u>Argyrosomus hololepidotus</u>. Cephalopods are shown by circles and fishes by crosses.

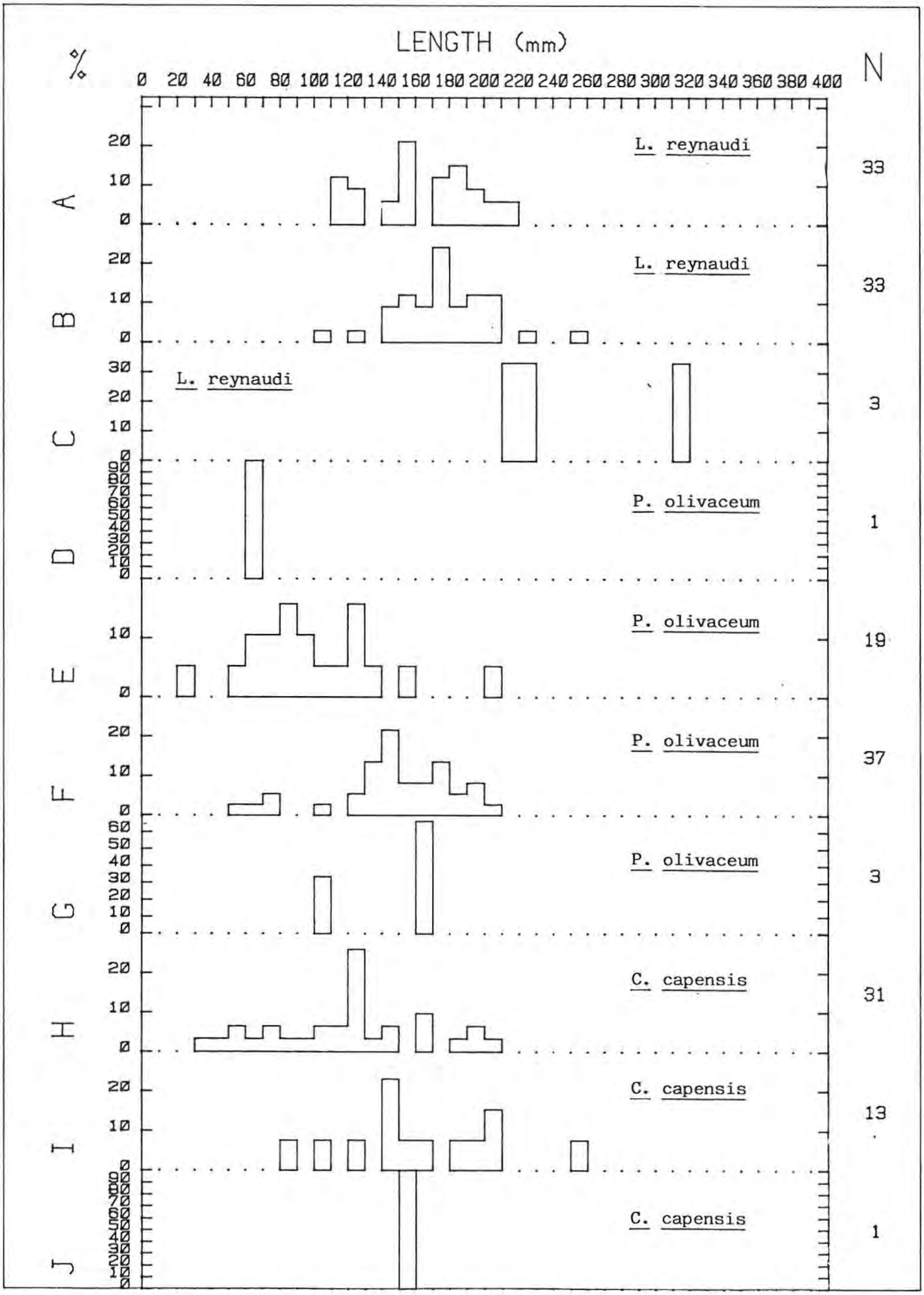


Fig. 39. Histograms of Loligo reynaudi (A,B,C); Pomadasys olivaceum (D,E,F,G) Cynoglossus capensis (H,I,J); taken by Argyrosomus hololepidotus of 201 - 300 mm (D); 301 - 500 mm (A,E,H); 501 - 1000 mm (B,F,I) and 1000 mm (C,G,J).

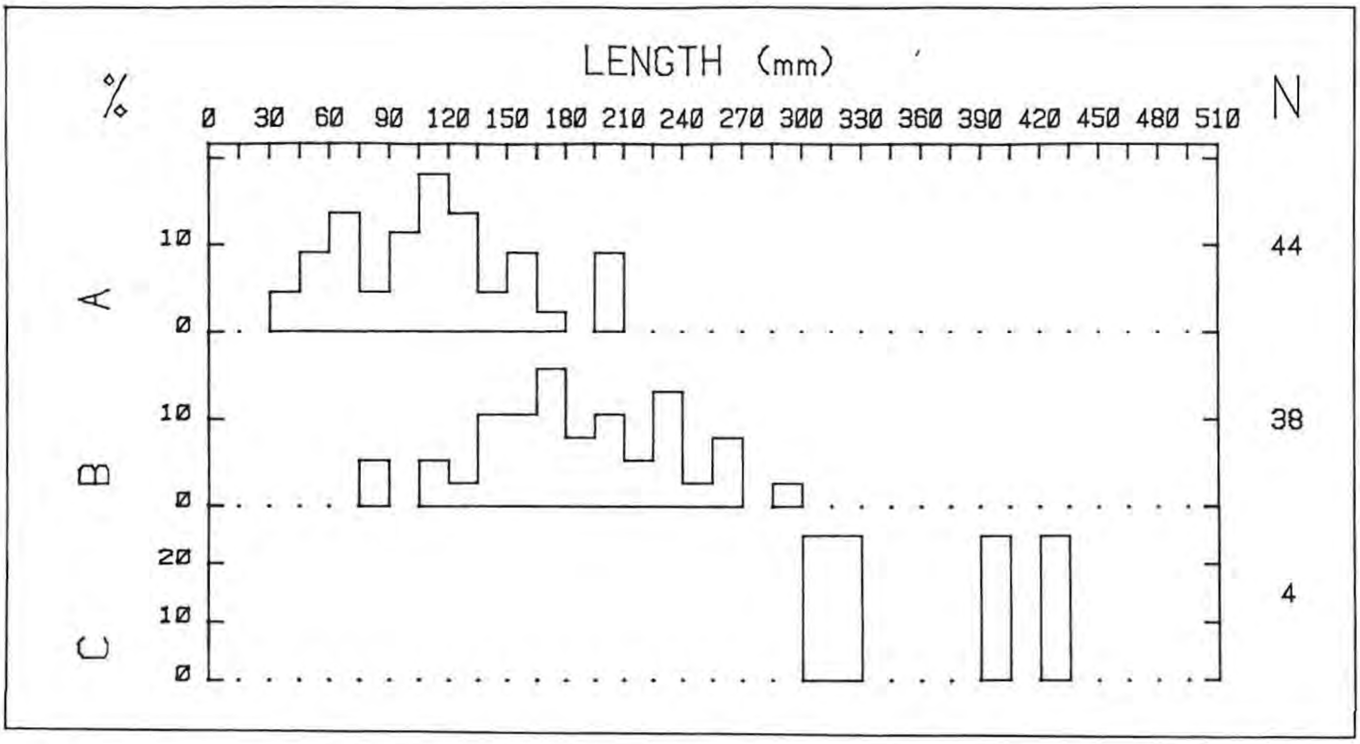


Fig. 40. Histograms of Argyrosomus hololepidotus cannibalised by fish of 301 - 500 mm (A); 501 - 1000 mm (B) and > 1000 mm (C).

groups, the larger specimens take larger prey than small kob. This trend is shown most clearly with P. olivaceum and A. hololepidotus as prey. With L. reynaudi and C. capensis the trend is less obvious.

In summary it seems that although potential intraspecific competition may be reduced by large fish being able to take bigger prey, A. hololepodotus takes a very wide size range of prey and has considerable overlap in prey size choice over much of the length range studied.

Prey selection and locality

The fish were divided according to size and area caught (Table 19). Area A is from the harbour around the edge of the bay to just beyond Sundays River, but including St Croix, Jaheel and Brenton islands. Area B is Riy Bank, Cape Recife, Noordhoek and Sardinia Bay. These are more exposed areas of the Bay and environs, where fish are often caught close to pinnacles and reefs. Area C includes Port Alfred and East London. Area D is Jeffreys Bay to Mossel Bay, where few fish were collected. Only two size groups were used as few small (<300 mm) or large (>1000 mm) specimens were collected .

In Area A, the prey of both the small and large kob show close similarity; both took mysids, L. reynaudi, G. feliceps, A. hololepidotus and P. olivaceum, in different proportions. Furthermore, the large group took more squid and fishes. The prey number and masses for each major category were:

	200 - 500 mm	501 - 1800 mm
Crustacea	99%N, 16%M	91%N, 1%M
Cephalopoda	<1%N, 21%M	1%N, 26%M
Pisces	1%N, 64%M	8%N, 73%M

In Area B mysids were considerably less important for small kob and were not taken at all by the larger fish. Loligo was more important here to both groups, but especially to large kob. Schooling pelagic fish, especially S. ocellata and E. capensis, were major prey of the small group but not to big kob which took mainly demersal fish such as Pomadasys olivaceum, Pagellus natalensis and S. salpa and A. sebastoides. It

Table 19 (a). The prey of Argyrosomus hololepidotus of 200 - 500 mm taken in three localities - see text for details. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	Area A %F	%N	%M	Area B %F	%N	%M	Area C %F	%N	%M
CRUSTACEA									
Unidentified crustaceans	1.1	<0.1	<0.1	6.7	1.7	0.9			
Copepoda	0.4	<0.1	<0.1				5.6	0.3	<0.1
Mysidacea	30.5	98.8	13.8	6.7	60.0	0.8	16.7	87.9	3.8
Caridea	0.4	<0.1	0.1						
Panaeidea	7.5	0.1	0.8	22.2	5.5	1.8	5.6	0.6	0.6
Brachyura	0.8	<0.1	0.1						
Megalopa larvae	0.4	<0.1	<0.1	6.7	1.7	0.3			
Anomura	0.8	<0.1	0.8	11.1	8.1	1.8	5.6	0.6	2.5
Callianassa sp.				6.7	1.3	1.8			
MOLLUSCA									
Sepiidae				11.1	2.1	5.2			
Loliginidae	0.4	<0.1	<0.1						
Loligo reynaudi	10.5	0.1	18.9	13.3	3.0	29.4	11.1	0.6	18.9
Octopoda (Benthic)	0.8	<0.1	0.2						
Octopus vulgaris	0.4	<0.1	1.6						
OSTEICHTHYES									
Unidentified fish remains	7.9	<0.1	2.7	11.1	2.6	5.0	22.2	1.8	5.7
Etrumeus teres	1.5	<0.1	1.0				5.6	0.3	2.5
Sardinops ocellata	3.4	<0.1	4.5	6.7	1.7	6.8			
Engraulidae	0.4	<0.1	<0.1						
Engraulis capensis	3.4	<0.1	1.4	15.6	6.4	29.2	11.1	0.6	10.1
Galeichthys feliceps	11.7	0.4	5.3	2.2	0.4	0.9			
Bregmaceros sp.							27.7	4.1	3.9
Merluccius capensis							5.6	0.3	0.8
Bothidae							5.6	0.6	15.1
Soleidae	0.4	<0.1	<0.1						
Cynoglossidae	0.4	<0.1	<0.1	2.2	0.4	0.2	11.1	0.6	6.3
Cynoglossus capensis	11.3	0.1	13.3	6.7	1.3	3.4			
Cynoglossus zanzibarensis	1.9	<0.1	1.8				16.7	1.2	24.3
Ammodytes capensis	0.4	<0.1	<0.1				5.6	0.3	1.0
Cheilodactylus pixi	0.8	<0.1	0.2						
Chirodactylus brachydactylus				2.2	0.4	0.2			
Trachurus trachurus	2.3	<0.1	2.2						
Pomatomus scaltatrix	0.8	<0.1	1.1						
Argyrosomus hololepidotus	17.7	0.2	18.2	2.2	0.4	4.1			
Umbrina canariensis	0.4	<0.1	1.5						
Pomadasys olivaceum	10.2	<0.1	7.8	2.2	0.4	1.4			
Rhonciscus striatus							5.6	0.3	4.5
Pagellus natalensis	0.4	<0.1	<0.1						
Scomber japonicus	0.4	<0.1	0.7						
Atherina breviceps				2.2	2.1	5.9			
Gobiidae	1.5	<0.1	<0.1	2.2	0.4	0.9			
Chatrabus melanurus	0.4	<0.1	1.5						
Totals	266	36849	2095.4	45	235	219.3	18	340	79.5

Table 19 (b). The prey of *Argyrosomus hololepidotus* of 501 - 1800 mm taken from four localities - see text for details. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	Area A %F	%N	%M	Area B %F	%N	%M	Area C %F	%N	%M	Area D %F	%N	%M
CRUSTACEA												
Mysidacea	5.4	90.9	0.5									
Panaeidea	7.4	0.5	0.1	8.3	3.4	<0.1						
Brachyura	0.7	<0.1	<0.1									
Megalopa larvae							6.3	9.7	0.1			
MOLLUSCA												
Sepiidae	0.7	<0.1	<0.1									
Loligo reynaudi	19.5	0.9	25.6	41.7	20.7	59.8	43.8	22.6	77.6			
Octopus vulgaris	0.7	<0.1	0.5	8.3	3.4	1.1						
CHONDRICHTHYES Unidentified elasmobranchs				8.3	3.4	3.8						
OSTEICHTHYES Unidentified fish	7.4	0.4	0.2	25.0	13.8	5.3	18.2	9.7	1.8			
Etrumeus teres	2.7	0.1	0.5									
Sardinops ocellata	5.4	0.2	4.5									
Engraulis capensis	2.0	0.1	0.2				6.3	12.9	6.0			
Galeichthys feliceps	14.8	3.4	1.4	8.3	20.7	0.1						
Bregmaceros sp.							6.3	22.6	0.1			
Merluccius capensis							6.3	3.2	4.3	33.3	28.6	34.6
Austroglossus pectoralis	0.7	<0.1	0.8									
Cynoglossidae	0.7	<0.1	0.1									
Cynoglossus capensis	8.7	0.4	3.6				6.3	3.2	0.1			
Ammodytes capensis	0.7	<0.1	0.1									
Cheilodactylus pixi							6.3	3.2	1.6			
Acanthistius sebastoides	1.3	<0.1	0.6	8.3	3.4	9.5						
Trachurus trachurus	1.3	<0.1	3.1									
Pomatomus saltatrix	1.3	<0.1	2.7							33.3	7.1	7.6
Scombrops dubius							6.3	3.2	7.0			
Argyrosomus hololepidotus	26.8	1.4	20.8									
Umbrina canariensis	0.7	<0.1	0.1									
Pomadasys olivaceum	26.2	1.1	18.0	16.7	13.8	2.9	6.3	6.5	0.5			
Lithognathus mormyrus										33.3	57.1	55.4
Pagellus natalensis	0.7	<0.1	0.9	8.3	6.9	13.7						
Rhabdosargus holubi	0.7	<0.1	0.4									
Sarpa salpa				8.3	10.3	3.8						
Scomber japonicus	4.0	0.3	15.3							33.3	7.1	2.5
Chelidonichthys queketti							6.3	3.2	1.0			
Totals	149	4140	5568.8	12	29	526.1	16	31	515.3	3	14	397

is significant that the latter two species occur on reefs. The major categories of prey were:

	200 - 500 mm	501 - 1800 mm
Crustacea	78%N, 7%M	3%N, <0.1%M
Cephalopoda	5%N, 35%M	24%N, 61%M
Pisces	17%N, 58%M	72%N, 39%M

In Area C in the vicinity of Port Alfred and East London, mysids were again dominant by number for small fish but not recorded in the large kob, which took crab megalopae. *L. reynaudi* was one of several important prey in small *A. hololepidotus*, and the single most important prey of those over 500 mm. *E. capensis*, *Bregmaceros* sp., Bothidae, and *Cynoglosus zanzibarensis* (a warm water cynoglossid) were the more important fish prey of small kob. The large size group also took *E. capensis*, *Bregmaceros sp*. In addition, they also took *M. capensis* and *S. dubius*, although teleosts were of secondary importance to cephalopods by mass.

The major groupings in Area C were:

	200 - 500 mm	502 - 1800 mm
Crustacea	89%N, 7%M	10%N, 0.1%M
Cephalopoda	1%N, 19%M	23%N, 78%M
Pisces	10%N, 74%M	68%N, 22%M

In Area D (areas west of Algoa Bay) only large *A. hololepidotus* were sampled. These had taken *M. capensis*, *P. saltatrix*, *L. mormyrus* and *S. japonicus*. Fish made up the entire diet in this area.

In summary, it is evident that the prey of kob differs according to locality and size.

Seasonality of prey selection

A bi-monthly analysis of prey taken is shown in Table 20. Mysids were taken by small fish (<500 mm) throughout the year, but were particularly dominant in March-April. At this time they were abundant in the diet of big kob but also occurred in November-December. Only two size groups were used as few very small (<300 mm) or very large (>1000 mm) kob were taken.

Table 20 (a). The prey of *Argyrosomus hololepidotus* of 200 - 500 mm taken in bi-monthly periods.
The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	January-February			March-April			May-June			July-August			September-October			November-December		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA																		
Unidentified crustaceans							3.1	0.1	0.1	2.8	2.2	0.3	18.2	1.2	1.6			
Copepoda										5.6	2.2	0.1						
Mysidacea	9.1	74.3	1.3	36.8	99.5	31.4	25.0	95.9	9.2	13.9	34.8	0.2	13.6	87.2	3.3	38.5	98.3	7.7
Caridea																1.3	<0.1	0.2
Penaeidea	6.1	0.9	1.0	4.2	<0.1	0.4	6.3	0.2	0.8	11.1	5.6	0.6	31.8	3.0	2.6	12.8	0.2	1.4
Brachyura	1.5	0.1	0.1	1.1	<0.1	0.3												
Megalopa larvae	1.5	0.3	0.1				3.1	0.2	0.3				4.5	0.3	0.2	1.3	<0.1	<0.1
Anomura				2.1	0.1	0.4	3.1	0.7	16.8	2.8	1.1	0.1				5.1	0.1	0.5
Callianassa sp.							6.3	0.2	1.2	2.8	1.1	0.7						
MOLLUSCA																		
Sepiidae	1.5	0.1	<0.1				3.1	0.1	1.0	5.6	2.2	2.6	4.5	0.3	0.1			
Loliginidae	1.5	0.3	0.1															
Loligo reynaudi	13.6	1.3	7.8				3.1	0.1	1.0	27.8	12.4	43.1				20.5	0.3	42.8
Octopoda (Benthic)	3.0	0.3	0.9															
Octopus vulgaris				1.1	<0.1	4.6												
OSTEICHTHYES																		
Unidentified fish	6.1	0.5	2.0	10.5	0.1	3.4	9.4	0.4	4.4	8.3	3.4	3.9	18.2	1.2	2.8	7.8	0.1	2.7
Etrumeus teres	3.0	0.4	1.4	1.1	<0.1	0.3										2.6	<0.1	2.4
Sardinops ocellata	9.1	0.9	9.3	3.2	<0.1	8.3										3.8	0.1	1.2
Engraulidae																1.3	<0.1	0.2
Engraulis capensis				7.4	<0.1	2.9	6.3	0.2	10.9	8.3	3.4	2.9	13.6	3.3	44.5	3.8	0.1	2.0
Galeichthys feliceps	30.3	14.5	17.4	9.5	0.1	4.5	9.4	0.4	3.5									
Bregmaceros sp.				5.2	<0.1	0.4												
Merluccius capensis				1.1	<0.1	0.1												
Bothidae				1.1	<0.1	1.7												
Soleidae										2.8	1.1	0.3						
Cynoglossidae							3.1	0.1	0.2	5.6	2.2	1.3	4.5	0.3	0.4			
Cynoglossus capensis	12.1	1.5	17.8	2.1	<0.1	0.2	21.9	0.9	17.5	25.0	18.0	36.4				9.0	0.2	7.5
Cynoglossus zanzibarensis	1.5	0.1	1.1	5.3	<0.1	5.3				5.6	3.4	3.9						
Ammodytes capensis				1.1	<0.1	0.1							4.5	0.3	0.2			
Cheilodactylus pixi				1.1	<0.1	0.4										1.3	<0.1	0.2
Chirodactylus brachydactylus													4.5	0.3	0.5			
Trachurus trachurus	4.5	0.4	2.1													3.8	0.2	5.8
Pomatomus saltatrix				1.1	<0.1	1.8										1.3	<0.1	1.6
Argyrosomus hololepidotus	19.7	2.5	21.3	24.2	0.1	24.9	6.3	0.3	7.4	2.8	1.1	0.2	4.5	0.6	30.7	10.3	0.2	12.1
Umbrina canariensis																1.3	<0.1	4.8
Pomadasys olivaceum	10.6	0.9	13.1	13.7	0.1	8.5	3.1	0.1	25.7	8.3	3.4	2.2				5.1	0.1	2.0
Rhonciscus striatus										2.8	1.1	0.9						
Pagellus natalensis.	1.5	0.3	0.1															
Scomber japonicus	1.5	0.1	3.2															
Atherina breviceps													4.5	1.5	12.9			
Gobiidae	1.5	0.1	<0.1	2.1	<0.1	0.1				2.8	1.1	0.5	4.5	0.3	0.3			
Tharbacus melanurus																1.3	<0.1	4.8
Totals	66	747	444.3	95	29483	720.7	32	987	101.1	36	69	385.7	22	329	100.9	78	5789	641.5

Table 20 (b). The prey of <u>Argyrosomus</u> <u>hololepidotus</u> of 501 - 1800 mm taken in bi-monthly periods. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

	January-February			March-April			May-June			July-August			September-October			November-December		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA																		
Mysidacea				15.9	96.9	2.7										2.0	33.6	<0.1
Penaeidea				9.1	0.1	0.3	5.6	1.3	0.2	12.5	6.3	<0.1	23.1	13.0	0.8	6.0	8.4	0.1
Brachyura	2.1	0.8	<0.1															
Megalopa larvae				2.3	0.1	<0.1												
MOLLUSCA																		
Sepiidae																2.0	0.7	<0.1
<u>Loligo</u> <u>reynaudi</u>	21.3	9.1	15.2	4.5	0.1	20.3	5.6	2.6	18.5	87.5	68.8	90.0	30.8	21.7	66.2	34.0	12.6	30.1
<u>Octopus</u> <u>vulgaris</u>	2.1	0.8	1.2				5.6	1.3	1.6									
CHONDRICHTHYES Unidentified fish																2.0	0.7	0.9
OSTEICHTHYES Unidentified fish				4.5	0.1	0.4	22.2	9.0	6.0				30.8	21.7	4.2	14.0	5.6	0.5
<u>Etrumeus</u> <u>teres</u>	2.1	0.8	<0.1													6.0	2.1	1.2
<u>Sardinops</u> <u>ocellata</u>				6.8	0.1	7.6	11.1	2.6	11.7							6.0	2.1	5.7
<u>Engraulis</u> <u>capensis</u>	2.1	3.3	1.3	4.5	0.1	0.7										2.0	0.7	<0.1
<u>Galeichthys</u> <u>feliceps</u>	12.8	37.2	0.4	22.7	1.4	2.7	22.2	56.4	10.6				15.4	8.7	0.6	2.0	1.4	0.1
<u>Bregmaceros</u> sp.				2.3	0.2	0.1												
<u>Merluccius</u> <u>capensis</u>				2.3	<0.1	2.1										2.0	2.8	6.0
<u>Austroglossus</u> <u>pectoralis</u>				2.3	0.1	4.1												
Cynoglossidae	2.1	0.8	0.1															
<u>Cynoglossus</u> <u>capensis</u>	4.2	2.5	2.5	11.4	0.1	4.5	16.7	6.4	4.5	25.0	18.8	7.6				4.0	2.1	1.3
<u>Ammodytes</u> <u>capensis</u>																2.0	0.7	0.3
<u>Cheilodactylus</u> <u>pixi</u>	2.1	0.8	0.3															
<u>Acanthistus</u> <u>sebastoides</u>	4.3	1.7	1.3													2.0	0.7	2.2
<u>Trachurus</u> <u>trachurus</u>	2.1	0.8	4.9													2.0	0.7	2.6
<u>Pomatomus</u> <u>saltatrix</u>																6.0	2.1	7.9
<u>Scombrops</u> <u>dubius</u>													7.7	4.3	10.8			
<u>Argyrosomus</u> <u>hololepidotus</u>	31.9	18.2	14.9	22.7	0.3	19.6	22.2	9.0	27.8				15.4	17.4	16.5	18.0	7.7	19.8
<u>Umbrina</u> <u>canariensis</u>							5.6	1.3	1.6									
<u>Pomadasys</u> <u>olivaceum</u>	29.8	13.2	21.5	34.1	0.5	32.7	16.7	6.4	12.0	12.5	6.3	2.3	15.4	13.0	0.9	14.0	7.0	5.2
<u>Lithognathus</u> <u>mormyrus</u>																2.0	5.6	9.6
<u>Pagellus</u> <u>natalensis</u>	4.3	2.5	5.2															
<u>Rhabdosargus</u> <u>holubi</u>				2.3	<0.1	2.0												
<u>Sarpa</u> <u>salpa</u>							5.6	3.8	5.4									
<u>Scomber</u> <u>japonicus</u>	6.4	6.6	30.9													8.0	2.8	6.3
<u>Chelidonichthys</u> <u>queketti</u>	2.1	0.8	0.2															
Totals	47	121	2318.9	44	3833	1033.9	18	78	367.4	8	16	673.1	13	23	333	50	143	2280.9

G. feliceps was most abundant in the January-February samples, but also occurred through to May-June. The large group took this species almost throughout the year. L. reynaudi was most dominant in August-September and November-December in the small kob. The large group took squid throughout the year although it dominated in the latter half of the year. Engraulis capensis was taken throughout the year either by big or small A. hololepidotus. C. capensis was taken almost throughout the year. Both the small and large groups of A. hololepidotus were cannibalistic almost throughout the year. P. olivaceum was taken by small kob throughout the year except September-October. It was taken by large kob throughout the year, most commonly in the first half of the year.

The variation in prey taken may result from varying relative abundance of the major prey species on account of movements of both predator and prey populations between habitats.

Annual variation

Table 21 lists the annual data for all sizes of A. hololepidotus. Large fluctuations in important prey are found, probably because of the proportion of kob caught in different areas. However, it is notable that S. ocellata decreases in importance between 1978 and 1980, while Engraulis is a more dominant prey after 1978. This agrees with information collected from pelagic predators and tends to suggest a change in relative abundance of these two species during the study period.

A field investigation of prey selectivity by Argyrosomus hololepidotus

Stomach content analysis provides invaluable data on prey taken by a particular predator, but cannot by itself describe selectivity. Data presented above have suggested that A. hololepidotus is capable of taking a variety of prey, although some species dominated. Whether this results from particular prey preference or variation in the relative abundance of different prey species will be investigated here.

An independent assessment of prey availability was provided by an inshore small mesh trawling survey in the eastern Cape in 1980. The research

Table 21. Annual variation in prey taken by *Argyrosomus hololepidotus* of 200 - 1800 mm. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	1978			1979			1980			1981/82		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Unidentified crustaceans				2.4	0.3	0.1						
Copepoda							1.1	<0.1	<0.1			
Mysidacea	41.3	98.5	6.1	5.6	72.6	0.3	28.4	99.0	6.7			
Caridea	1.3	<0.1	0.2									
Penaeidea	14.7	0.4	1.1	8.3	1.4	0.3	6.3	<0.1	0.2			
Brachyura				0.4	<0.1	<0.1	1.1	<0.1	0.1			
Megalopa larvae				1.2	0.2	<0.1	1.1	0.1	<0.1			
Anomura				3.2	1.3	0.5						
Callianassa sp.							1.7	0.1	0.1			
MOLLUSCA												
Sepiidae				1.6	0.2	0.1	1.1	<0.1	0.2			
Loliginidae				0.4	0.1	<0.1						
Loligo reynaudi	16.0	0.2	19.9	14.2	1.9	24.5	14.8	0.1	30.8	50.0	42.9	62.0
Octopoda (Benthic)				0.4	<0.1	<0.1	0.6	<0.1	0.1			
Octopus vulgaris	1.3	<0.1	0.7	0.4	<0.1	0.6	0.6	<0.1	0.9			
CHONDRICHTHYES												
Unidentified elasmobranchs				0.4	<0.1	0.5						
OSTEICHTHYES												
Unidentified fish	12.0	0.2	3.6	9.9	1.2	1.0	6.8	0.1	1.2	16.7	14.3	0.7
Etrumeus teres				2.0	0.2	0.6	2.3	<0.1	0.7			
Sardinops ocellata	10.7	0.2	28.4	4.4	0.6	2.6	0.6	<0.1	0.1			
Engraulidae				0.4	0.1	<0.1						
Engraulis capensis	1.3	<0.1	0.6	4.0	1.0	2.2	6.3	<0.1	1.0			
Galeichthys feliceps	4.0	0.2	0.6	15.1	8.7	3.0	8.0	0.3	1.5			
Bregmaceros sp.							3.4	0.1	0.1			
Merluccius capensis							1.7	<0.1	4.2			
Bothidae							0.6	<0.1	0.3			
Soleidae				0.4	<0.1	<0.1						
Austroglossus pectoralis							0.6	<0.1	1.1			
Cynoglossidae				0.8	0.1	<0.1	1.7	0.1	0.2			
Cynoglossus capensis	4.0	0.1	3.8	9.9	1.6	4.1	10.8	0.1	7.2			
Cynoglossus zanzibarensis				0.4	<0.1	0.1	4.0	<0.1	1.4			
Ammodytes capensis	1.3	<0.1	0.8	0.4	<0.1	<0.1	0.6	<0.1	<0.1			
Cheilodactylus pixi				0.8	0.1	0.1				16.7	14.3	2.6
Chirodactylus brachydactylus				0.4	<0.1	<0.1						
Acanthistius sebastoides				0.4	<0.1	1.1	1.1	0.1	0.8			
Trachurus trachurus	1.3	0.1	7.0	1.6	0.6	3.4	1.7	0.1	0.2			
Pomatomus saltatrix				0.4	<0.1	0.2	1.7	<0.1	4.3	16.7	14.3	9.8
Scombrops dubius				0.4	<0.1	0.8						
Argyrosomus hololepidotus	4.0	0.1	9.0	22.6	3.7	16.6	15.9	0.1	19.3			
Umbrina canariensis	1.3	0.1	0.7	0.4	<0.1	0.7						
Pomadasys olivaceum	5.3	0.1	2.8	16.7	2.3	16.7	13.1	0.1	9.2	16.7	14.3	24.9
Rhonciscus striatus							0.6	<0.1	<0.1			
Lithognathus mormyrus							0.6	<0.1	5.7			
Pagellus natalensis				0.8	0.1	1.1	0.6	<0.1	1.9			
Rhabdosargus holubi				0.4	<0.1	0.5						
Sarpa salpa	1.3	0.1	2.3									
Scomber japonicus	1.3	0.1	12.5	2.0	0.5	16.9	1.1	<0.1	0.6			
Atherina breviceps				0.4	0.2	0.3						
Gobiidae				1.6	0.2	0.1	0.6	<0.1	<0.1			
Chelidonichthys queketti				0.4	<0.1	0.1						
Tharbacus melanurus				0.4	<0.1	0.7						
Totals	75	5936	858.5	252	2164	4407.1	176	33531	3830.6	6	7	305

vessel Thomas B. Davie was commissioned by the Port Elizabeth Museum to investigate the occurrence of juvenile estuarine associated species in inshore waters (Wallace et al. in prep.). The principal sampling gear used was a 20 m otter trawl of 50 mm stretch-mesh. The 3 m cod end was lined with 12 mm stretch-mesh knotless anchovy netting. Wooden otter boards of 1.7 x 0.88 m were used (Wallace et al. in prep.). The trawl catch made in Algoa Bay was used in this study. Trawls were confined to soft substrates to avoid gear damage. Stations deeper than 30 m were precluded as this is the maximum depth from which kob were collected with stomach contents. From the quarterly surveys, catches made in February and May were combined and compared to the prey of A. hololepidotus caught by line fishermen in the same area. Considerable differences were noted in catches made at different trawl stations and depths although the causes of these differences were not clear. The use of the two trawl surveys at the beginning of the year co-incided with the largest ski-boat catches of kob and reduced seasonal variability. Trawling depths and times varied and a total of 105 minutes was spent at less than 15 m and 79 minutes at stations between 15 and 30 m. The bias towards shallower water is also reflected by the A. hololepidotus stomach material as there is an increased likelihood of regurgitation with depth. As it was not possible to gauge the depth from which line-caught kob were collected, the trawl data was not weighted according to times trawled at different depths. As the mesh size of the net allowed small crustaceans to pass through, it was necessary to examine only the teleost and cephalopod component. To reduce the influence of an increase in maximum prey size taken by predators, the size group of 501 - 1000 mm was used. The maximum prey size taken over this range is similar, about 300 mm. Because large prey are unavailable to this group they were subtracted from the trawl catch.

The study sample therefore consisted of 90 A. hololepidotus of 501 - 1000 mm caught by line-fishermen between the Port Elizabeth harbour wall and Bird Island, Algoa Bay from January to June in 1978 to 1981. They had taken 250 fish and cephalopod prey. This material was compared to 13550 fish and cephalopods smaller than 300 mm taken by trawling in February and May 1980.

Selectivity was calculated using a modification of the Shorigin index proposed by Berg (1979). The formula is:

$$\mathrm{Sel} = \log_{10} \frac{\%\ \mathrm{Ni\ in\ the\ ingested\ food}}{\%\ \mathrm{Ni\ \ in\ the\ potentially\ available\ food}}$$

This modification overcomes the weighting of food preference over the food avoidance (Berg 1979). Conversion of this logarithmic food selection index to the original Shorigin index "k" is performed with the formula:

$$K = 10^{\mathrm{Sel}}$$

Ranges in the scale vary from complete avoidance which is given a value of $-\infty$ to consumption of food not sampled by the net which is given a value of $+\infty$. "Random" feeding receives the value of 0 in the centre of the scale (Berg 1979). The sizes of the principal components of the trawl and kob diet are compared and discussed.

Species occurrence

The percentage number of trawled fish is shown by closed bars and the percentage number taken by A. hololepidotus by open bars in Fig. 41A. Fourteen species contributed <0.1% of the trawl catch or less and are not shown in the figure if not taken by kob. These species were: Solea bleekeri, Cheilodactylus pixi, Cheilodactylus brachydactylus, Priacanthus hamrur, Cheimerius nufar, Rhabdosargus globiceps, Spondyliosoma emarginatum, Atractoscion aequidens, Amblyrhynchotes honckenii, Sphyraena africanum, Chelidonichthyes capensis, Chelidonichthyes kumu, Trichiurus lepturus, Sygnathus acus.
The difference in the numbers under consideration (13 550 trawled specimens against 250 taken by A. hololepidotus) suggests that rarely caught fishes would not be found in predators' stomachs unless they were highly preferred. As A. hololepidotus shows no evidence of a preference for them, their absence in kob stomachs is probably attributable to differences in sample sizes so they are not considered further.

Selectivity

Fig. 41B shows that among the four dominant species, A. hololepidotus prefers G. feliceps, A. hololepidotus and P. olivaceum but avoids P.

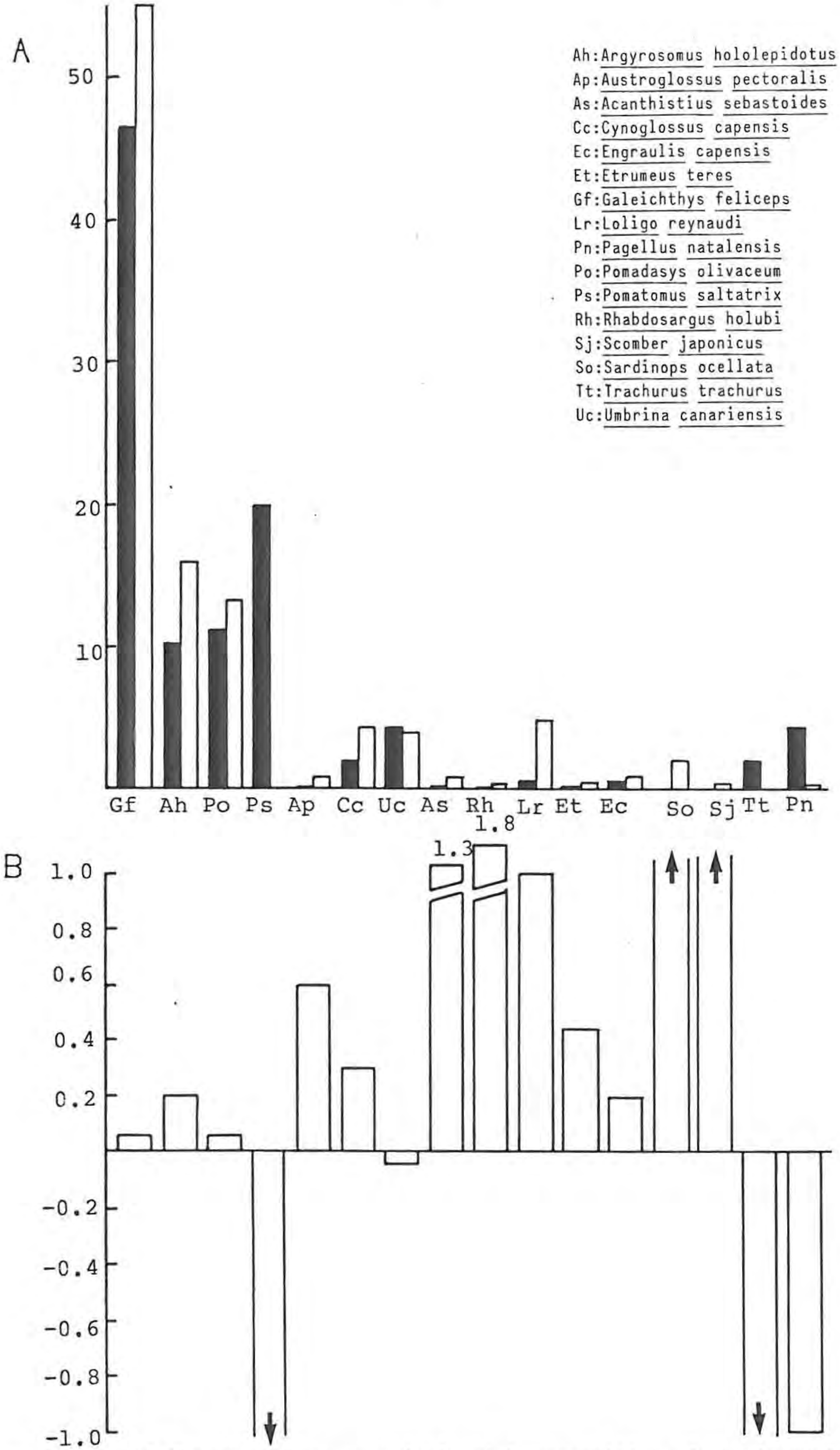


Fig. 41. A) The percentage numerical catch composition of trawl catches (closed bars) made in Algoa Bay at 7-30 m in February and May 1980 and the percentage numerical prey taken by Argyrosomus hololepidotus of 501 - 1000 mm in Algoa Bay (Area 1) between January and June 1978-1981.

B) Selectivity of A. hololepidotus of 501 - 1000 mm.

saltatrix completely. There is strong preference for Austroglossus pectoralis and Cynoglossus capensis but slight avoidance of Umbrina canariensis. There is very high selection for A. sebastoides, R. holubi and L. reynaudi and slight preference for Etrumeus teres and Engraulis capensis. S. ocellata and S. japonicus were not taken by trawling while T. trachurus and A. aequidens were caught by the trawl but not recorded in A. hololepidotus' stomachs. P. natalensis is apparently avoided by A. hololepidotus.

Length frequencies of common prey

In Fig. 42 the catch of G. feliceps trawled down to 30 m is shown for all stations considered and is separated below according to two arbitrary depths. Small sea-catfish are clearly found in shallow water while larger fish occur in deeper water. The A. hololepidotus size group under consideration (501 - 1000 mm) took only small sea-catfish (<110 mm) with a modal length of 60 - 70 mm. Juvenile G. feliceps were extremely abundant in trawls in February while those taken by kob were taken over a longer period. The increased range may reflect growth and, possibly, preference for slightly larger specimens. For comparative purposes the G. feliceps taken by the small size group of A. hololepidotus in Algoa Bay is shown and although a wider ranger is again evident (up to 100 mm), the modal size corresponds with trawl-caught fish.

The length frequency of A. hololepidotus (smaller than 300 mm) taken by trawls to 30 m is shown over the depth range to 30 m and according to two arbitrary depths in Fig. 43. Small kob were more common in the shallow areas. Two modes at 110 - 120 mm and 170 mm were evident in shallow areas while the principal mode at deeper stations was 160 - 170 mm. The prey of the kob under consideration (501 - 1000 mm) has a broad peak at 150 - 170 mm, showing that prey could have been taken at either depth range. If taken in shallow water, there may be a preference for larger fish; if taken in deeper areas prey may be taken according to abundance with no size selection. Conversely, small kob (300 - 500 mm) either show a pronounced selection in deep water or a less marked selection in shallow areas.

Examination of trawled P. olivaceum catches shows that this species appears to be relatively more common in shallow water and that larger fish

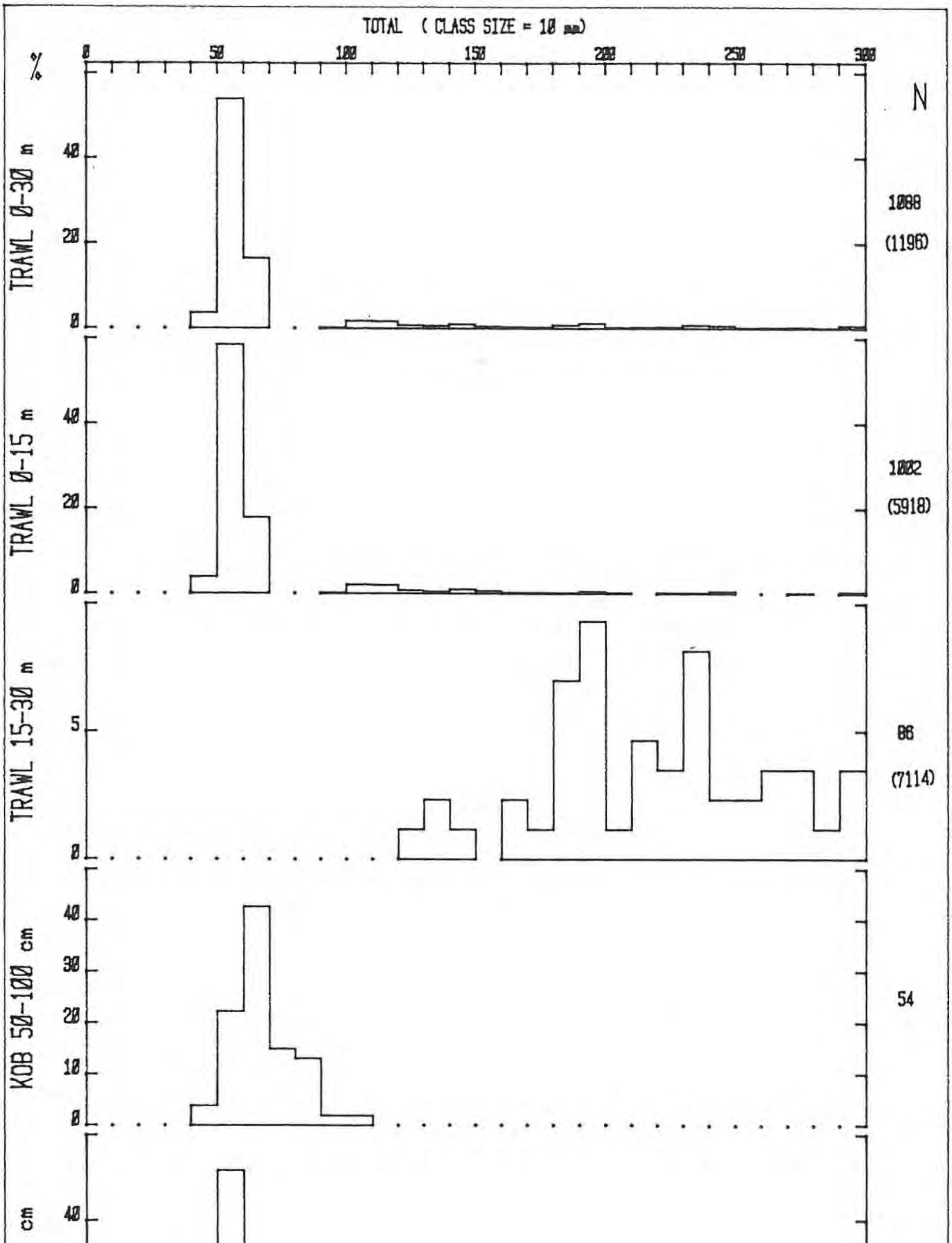


Fig. 42. Histograms of Galeichthys feliceps taken by trawl at different depths and by A. hololepidotus of different sizes. N is the number of fish measured, numbers in brackets are the totals trawled from the stations under consideration.

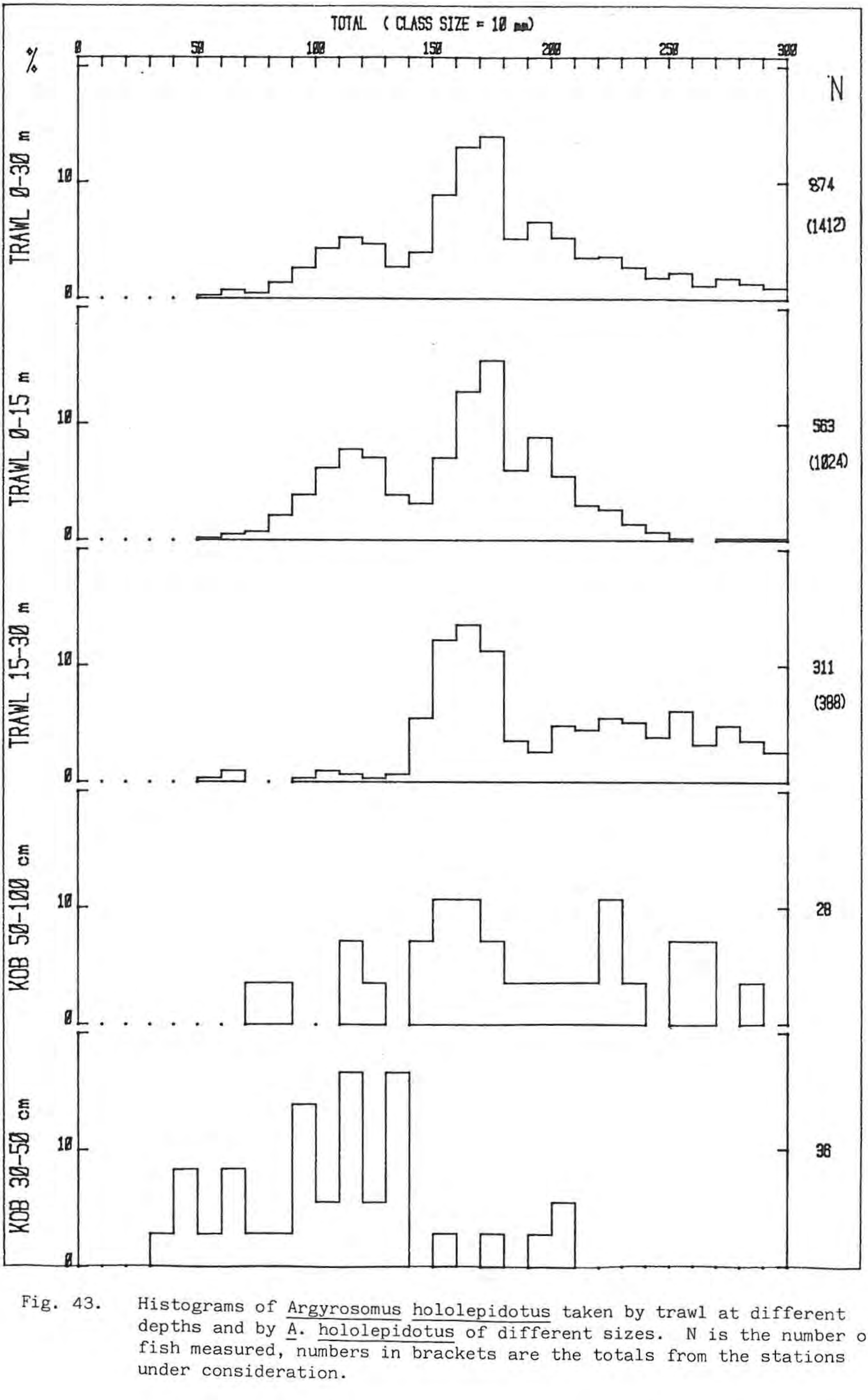


Fig. 43. Histograms of Argyrosomus hololepidotus taken by trawl at different depths and by A. hololepidotus of different sizes. N is the number of fish measured, numbers in brackets are the totals from the stations under consideration.

tend to dominate catches from deeper areas (Fig. 44 and Buxton in prep.). The large kob (501 - 1000 mm) took P. olivaceum between 60 and 210 mm, with a mode of 140 - 150 mm. These could have been taken from either deep or shallower areas although they would have selected for large fish and against small fish in the shallows. The smaller A. hololepidotus predators (300 - 500 mm) took P. olivaceum between 20 and 210 mm with a broad mode between 60 and 90 mm and another peak between 120 - 130 mm. These small fish would have been more commonly encountered in the shallows.

Discussion

The deep body, truncate tail and relatively deep caudal peduncle of A. hololepidotus suggest that this is a relatively slow-moving species (Norman & Greenwood 1963). However, the copious production of mucus through the skin, which is evident when one handles specimens, may partially off-set this; in addition to other functions, the substance is known to reduce drag as fish swim (Lagler et al. 1977). Drag reduction is particularly important during hunting, when bursts of speed are necessary for the predator to outswim the prey. Kob usually occur in schools, especially when small, and probably benefit by hunting schooled prey; many of the prey species identified in this study were schooling demersal species. The silvery to dark body colouration acts as camouflage by counter shading and darker colouration occurs most frequently in specimens found in turbid water. The function of the silver spots along the lateral line is not clear but their close association with the lateral line suggests that they may be specialised pressure receptors which are required for hunting where visibility is restricted. The lateral line terminates at the end of the caudal fin and probably aids in the detection of predators and prey in dirty water. Its preference for turbid water is also evident in estuaries (Wallace & van der Elst 1975, Kok pers.comm., Marais pers. comm., Whitfield & Blaber 1978). Davis & Miller (1967) found that minnows inhabiting turbid water have a large number of cutaneous taste buds, reduced optic lobes and several features which would aid non-visual prey location. On the other hand, those fish living in clear water locate food visually and have few taste buds. A. hololepidotus is also likely to be similarly adapted to low visibility hunting.

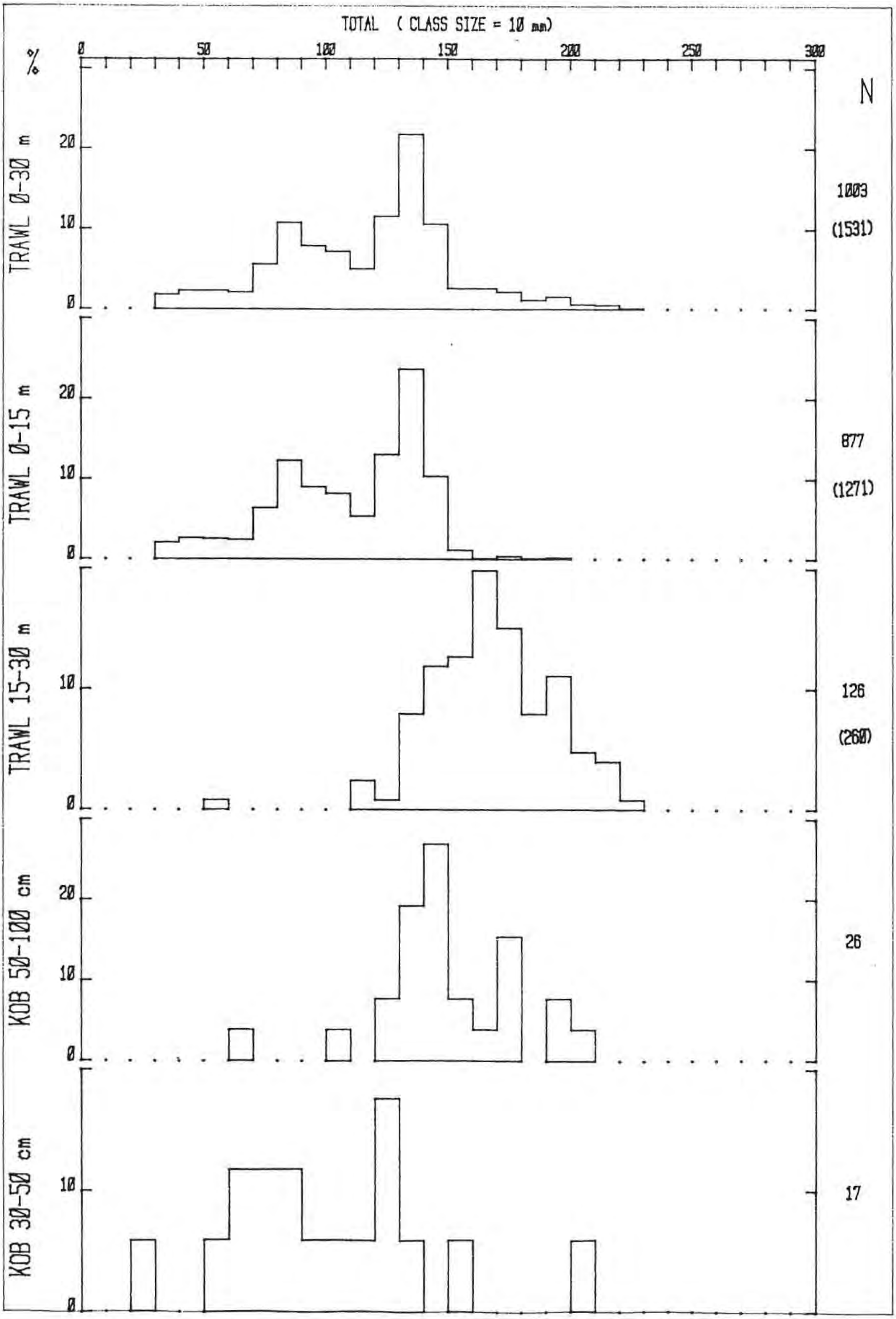


Fig. 44. Histograms of Pomadasys olivaceum taken by trawl at different depths and by A. hololepidotus of different sizes. N is the number of fish measured, numbers in brackets are the totals trawled from the stations under consideration.

There is some evidence that kob exhibit size segregation according to depth. Wallace & van der Elst (1975) and Whitfield & Blaber (1978) found that large kob stayed in the deeper waters of Lake St Lucia while smaller specimens entered the shallows more readily. However, this sytem is very shallow throughout (< 2 m). Whitfield & Blaber (1978) attributed their depth preference to threat of attack by fish eagles, prevention of cannibalism, prevention of over exploitation of prey and the distribution of aquatic macrophytes. In addition, the threat of stranding must be great in such a shallow system. The length distribution of A. hololepidotus trawled in Algoa Bay showed a similar pattern. Smaller fish were abundant in the shallows (Fig. 43 & Smale in prep.) and the modal size increased with depth. These trawls were made by day and it is possible that the predators move inshore at twilight and at night, as has been found for sharks (Wallett 1978), freshwater catfish (Bruton 1979) and several tropical reef predators, although Hobson (1973) believes that relatively few tropical predators are active at night. It is quite likely that factors affecting predation by tropical reef fishes are very different in the turbid, and spatially less complex in warm temperate seas. Nevertheless, some behavioural patterns will be common to both. Examples are prey schooling to avoid predation (Stark & Davis 1966, Hobson 1968, Potts 1969, 1970, Hobson 1973, Radakov 1973, Bruton 1979, Potts 1980, 1981, and Chapter 4) and movement within their habitat (e.g. Hobson 1968, 1973, Lasiak 1982).

Evidence that A. hololepidotus does move inshore in the evening is provided by beach anglers who catch more by night than at mid-day (pers.obs.). Lasiak (1982) also found that kob move into the surf-zone at night. These specimens may be very large. B.E. Trow (Department of Ichthyology and Fisheries Science, Rhodes University,pers.comm.) has made the following observations. A large specimen estimated at 2 m long was observed swimming in water 1 m deep on a moonless night in the summer of 1979/80 at Coffee Bay, Transkei. On another occasion a kob of about 2 m was found in a closed tidal pool at night, feeding on a trapped school of Sarpa salpa. The observations show that A. hololepidotus does enter shallow water and feeds there, especially at night. Furthermore, the occurrence of large fish in estuaries (Day & Morgans 1956, Wallace 1975, Whitfield & Blaber 1978) clearly shows that the depth preference is not rigid and may depend on prey distribution. The relatively low number from surf-zone samples suggests that deeper areas are preferred. Lasiak (1982) found that they made up about 4% of the total surf-zone catch.

A.hololepidotus selects a wide range of prey species, varying from small crustaceans to demersal and pelagic fish. Small crustaceans especially penaeids and mysids dominated the prey of *A. hololepidotus* of 200 - 300 mm TL. An independent study of predation by small trawl-caught *A. hololepidotus* (<200 mm) (Smale in prep.) found that the mysids, especially *Mesopedopsis slabberi*, were the most important prey. *M. slabberi* is a common inshore species found over a wide variety of substrates and even enters estuaries (Tattersall & Tattersall 1951, Wittmann 1977, Woolridge, University of Port Elizabeth, pers.comm.). It occurs in extremely large swarms in Algoa Bay and is an important prey of several other juvenile fish species (Smale in prep.). Mysids were found in the stomachs of kob up to about 656 mm. This is explained by the compact swarms characteristic of *M. slabberi* (Wittmann 1977). Rather than being a plankton picker, *A. hololepidotus* obviously takes large mouthfuls of this prey, making mysids more rewarding energetically. These findings suggest that mysids, and particularly *M. slabberi*, are extremely important prey in the eastern Cape.

The importance of crustaceans in the diet of *A. hololepidotus* has also been observed in other studies. Thirteen kob of 207 - 384 mm caught in Durban harbour had taken penaeid prawns, the crab *Hymenosoma* and fish (Day & Morgans 1956). Whitfield & Blaber (1978) recorded that crustaceans made up 17.6% of the number and 6.3% of the mass of prey taken in Lake St Lucia estuary. Lasiak (1982) found that crustaceans constituted 20.3% of the prey wet mass taken from Kings Beach, Algoa Bay, although here mysids were of minor importance (0.04%). The prawn *Macropetasma* was far more dominant, making up 19.2% of the wet mass and occurring in 48.1% of the stomachs examined. At Bluewater Bay near Swartkops River, Lasiak (1982) found that crustaceans made up 30.7% of the wet mass of prey and *M. slabberi* was more important, making up 7.7% of the wet mass (predator size range, 148-452 mm).

Although crustaceans were taken by *A. hololepidotus* in each of the size-groups in the present study, cephalopods and fish were found to dominate the diet of kob larger than 300 mm. Schooling squid (*L. reynaudi*) and fish, for example S. ocellata, E. capensis, M. capensis, T. trachurus and P. olivaceum were important prey. They are both pelagic and demersal schoolers which would probably be most successfully attacked by schooling predators (see Chapter 4). A. hololepidotus usually occurs in schools of similar-sized fish although individuals may be observed on occasion (pers.obs., Whitfield & Blaber 1978). When alone, individual prey items such as Gobiidae, Chatrabus melanurus and cynoglossids may be taken more efficiently.

The hunting behaviour of kob has not been recorded in detail because they appear to be at least partially nocturnal (Lasiak 1982, pers.obs.) and favour turbid water. They are also caught during the day by line fishermen and prey of day-caught kob often appeared to be recently ingested. The occurrence and importance of feeding periodicity is therefore unknown.

The large number of teleost species taken by A. hololepidotus is partly a reflection of its wide choice of habitats. It was shown earlier that prey selection varies between areas. This would tend to reduce potential intraspecific competition by reducing the predators' impact on a particular species. It is noteworthy that Lithognathus mormyrus was taken most frequently west of Algoa Bay, where it is known to be most common (Buxton in prep.). Similarly, L. reynaudi was taken in areas where it is common in the diet of other predators. This implies that prey are taken in proportion to their abundance, as has also been found by Whitfield & Blaber (1978). These authors found that A. hololepidotus responds to an increase in the abundance of Gilchristella aestuarus by feeding on it more frequently. Similarly, they found that when penaeid prawns were more abundant during summer, they contributed up to 70% of the diet. This behaviour would partially account for changes in prey selection during the year and between different years.

Cannibalism was a noteworthy feature of predation by A. hololepidotus. It was shown that A. hololepidotus of 301 - 500 mm (about 1-2 years old) preyed on kob of 36 - 209 mm (0y), according to age studies of Wallace & Schleyer (1979). The 501 - 1000 mm group (2y-6y) took kob of 79 - 288 mm (0-1y) while those of 1001 - 1800 mm (6->12y) took kob of 314 - 425 mm (2y). Only 10% of A. hololepidotus caught by ski-boats were larger than 600 mm

TL, suggesting that the greatest predation will be on kob of 0 years (<230 mm). At this age mysids and other crustaceans are the major prey. Cannibalism in A. hololepidotus would reduce particularly strong year classes and would effectively decrease the likelihood of intra-specific competition. These observations accord with those of previous studies (Davies 1949, Richards 1976, Helfman 1978, Macpherson 1980, and this study of P. saltatrix and M. capensis). Fox (1975) reviewed cannibalism in natural (i.e. not laboratory) populations and noted that it is often a response to population density and food availability, but that several factors may interact. As discussed below, it seems that small kob may be taken in a density-dependent way (although possibly preferred) and it was noted that Algoa Bay (mainly between the harbour wall and Bird Island) was the principal place where juvenile kob were cannibalised. This needs confirmation by more intensive sampling along other areas of the east and south Cape coast, but it suggests that Algoa Bay is a major nursery area, as has been confirmed during a trawling survey there (Smale in prep.). It is interesting to note that the depth preferences postulated by Whitfield & Blaber (1978) to prevent cannibalism in estuaries, do not hold in the sea, perhaps because the larger population in the sea results in higher contact rates and juvenile kob apparently do not use the shallow surf zone in the sea (Lasiak 1982) as they are able to use the shallows in estuaries. This may be correlated with prey distribution. It is not possible to quantify the effect of cannibalism in the sea because there is no information on feeding rates, movements of large and small fish or their abundance in the shallows. Given the importance of this species to the line and trawl fishery, the current interest in marine nurseries and the accessibility of a suitable study area, an intensified investigation of cannibalism is urgently needed.

Prey selectivity

This field study of prey selectivity has shown that the most numerous prey available are taken in a density dependent manner. This clearly holds for G. feliceps, A. hololepidotus and P. olivaceum. The complete absence of P. saltatrix in kob stomachs suggests that they are capable of outswimming this relatively slow predator, although they have occasionally been taken by kob in other areas during this study. On the other hand, the two flatfish, Austroglossus pectoralis and Cynoglossus capensis, were positively selected. These two species hide by camouflaging themselves on or just under the substrate, but it appears that *A. hololepidotus* is able to detect and capture them. Whether they are detected by scent or other cues is unknown.

The apparently strong selection for *Acanthistius sebastoides* is an artifact caused by trawling being confined to sandy areas and avoiding reefs where this species is found. *Rhabdosargus holubi* is rarely encountered in marine waters (pers.obs. & Kok *et al*. in prep.) and the apparently strong selection is probably attributable to kob which have recently returned to the sea from estuaries where *R. holubi* is a dominant component of the fauna (Talbot 1955, Blaber 1974, Winter 1980).

The marked selection for *L. reynaudi*, *E. teres*, *S. ocellata* and *S. japonicus* but strong avoidance of *T. trachurus* may in part be artifacts caused by the difficulty of catching these species in demersal trawl nets, even in relatively shallow water. These species also school and are patchily distributed, making it unlikely that they would be sampled in proportion to their abundance with limited trawling. In addition, it was shown earlier that *S. ocellata* was very abundant during 1978 but less common in subsequent years (Chapter 4). A similar pattern was found with predation by kob, which could explain the absence of pilchard from the net but their presence in stomach contents collected over several years. The effects of diurnal changes in distribution of *Loligo reynaudi* is unclear, but may result in the squid not being equally available to trawls and kob. Furthermore, it is likely that squid are particularly vulnerable to predation during spawning (Chapter 4).

Despite being a small demersal schooling species which has been recorded in kob stomach contents from other areas, *Pagellus natalensis* was avoided by kob in the selectivity investigation. This may result from a preference for flatfish and kob. Alternatively it may reflect differences in microhabitat selection and thus a low encounter rate, as has been proposed in other systems (Whitfield & Blaber 1978). These authors attributed the low occurrence of *Rhabdosargus holubi* in the diet of *A. hololepidotus* in Lake St Lucia to the prey hiding in littoral macrophyte beds.

Examination of the length range of important prey species revealed some interesting but apparently contradictory results. The large *A.*

hololepidotus (501 - 1000 mm) took a length frequency of kob which strongly resembled those trawled from stations 15 - 30 m deep, while small A. hololepidotus (300 - 500 mm) took prey most similar to the length frequency of kob trawled from the shallows. This pattern was again shown in the predation on P. olivaceum. The results suggest that A. hololepidotus of different sizes hunt at different, preferred depths, where prey is taken opportunistically. Alternatively, there is marked selection for a preferred size range by different sized predators, which may hunt independently of depth. Evidence for depth preferences was provided during the Thomas B. Davie cruises where a trend of increased modal size with depth was found during day trawls. This agrees with Wallace & van der Elst (1975) and Whitfield & Blaber (1978) that large kob at Lake St Lucia and other estuaries prefer deep water. Conflicting evidence is provided by inshore forays, particularly at night (Lasiak 1982, see above). Further conflicting evidence is provided by the predation by large kob on small G. feliceps, which are apparently restricted to very shallow water.

In synthesis, these two interpertations may not be incompatible. During the day the apparent depth preference of A. hololepidotus may be partly governed by prey distribution. This has been suggested by Blaber & Blaber (1980) to account partially for the distribution of juvenile teleosts off Queensland. The prey species in turn select areas where they may best balance the conflicts of avoiding predation and obtaining food. This often involves migrations by schools between microhabitats (Hobson 1973, Bruton 1979, Lasiak 1982), and feeding when predation risk is lowest. A. hololepidotus seems particularly adapted to preying on those teleosts favouring turbid water to reduce predation (Blaber & Blaber 1980). At night, however, large A. hololepidotus appear to move into shallow water and use prey resources not taken by day, including G. feliceps. It is possible that A. hololepidotus follows prey species in their migration to nocturnal feeding grounds. This has been found by Hobson (1968) for other predators and may partially account for diurnal changes in the relative abundance of P. olivaceum in the surf-zone (Lasiak 1982).

In summary, it is clear that A. hololepidotus is capable of taking a wide variety of prey, ranging from small crustaceans to relatively large fish.

It is adapted to feeding in turbid water yet retains a behavioural plasticity, allowing it to attack solitary or schooling prey. Size-related depth distribution may be related to prey distribution and, probably, avoidance of predation by day, when kob may be seen near reefs and wrecks although it is still commonly caught over sand. At night the predators appear to move inshore and feed on prey which may not be available by day. Although similar prey are taken by kob larger than 300 mm, the potential for intraspecific competition is reduced by differences in diurnal depth distribution, a preference for larger prey by big kob and the use of highly abundant prey when available. A. hololepidotus uses a wide variety of habitats and a wide depth range.

Other demersal predators

A hololepidotus is clearly a very dominant fish of shallow sandy substrates. Juveniles share resources, particularly mysids, with Pomatomus saltatrix juveniles (Smale in prep.) and other species such as P. olivaceum (Buxton in prep.), as well as a large number of other small fish. However, this prey is highly abundant in the shallows (Tattersall & Tattersall 1951, Woolridge pers.comm.) so it is not certain that these fishes are competing for prey (Sale 1979). As it grows, A. hololepidotus exploits a wider variety of resources, demersal and pelagic fishes becoming more important. Another teleost which takes similar prey is Merluccius capensis, as may be seen from the small sample collected largely from commercial trawlers which had been fishing near Algoa Bay (Table 22). This agrees with data collected by Hecht (1976). The species is commercially important in this region but is commonly found in deeper waters (Hecht 1976, Smale in prep.). The large size of the M. capensis population suggests these two species may compete for prey if food is limiting. Competition must be reduced by the different depth preferences although Hecht (1976) has recorded that these species may co-occur in the same trawls at depth. It is interesting to note that in addition to cannibalism being exhibited by both species, each also preys on the other species.

It seems likely that sharks, particularly the Carcharhinidae, share the same resources over sandy substrates, which are ideal areas for them to hunt. Although data are not available for the eastern Cape, information presented by Bass et al. (1973, 1975a,b,c,d, 1976) and van der Elst

Table 22. The prey of *Merluccius capensis*. The totals are numbers of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	%F	%N	%M
CRUSTACEA			
Unidentified crustaceans	2.0	1.1	< 0.1
Penaeidea	2.0	1.1	< 0.1
Megalopa larvae	3.9	23.4	0.3
MOLUSCA			
Loligo reynaudi	3.9	2.1	2.1
Lycoteuthis diadema	2.0	1.1	0.4
OSTEICHTHES			
Unidentified fish	5.9	3.2	2.2
Etrumeus teres	3.9	2.1	1.1
Sardinops ocellata	58.8	36.2	61.4
Engraulis capensis	21.6	13.8	6.6
Merluccius capensis	7.8	5.3	9.8
Cynoglossus capensis	7.8	4.3	4.6
Acanthistius sebastoides	2.0	1.1	0.2
Trachurus trachurus	2.0	1.1	4.2
Argyrosomus hololepidotus	3.9	2.1	4.0
Spariidae	2.0	1.1	3.0
Pagellus natalensis	2.0	1.1	0.1
Totals	51	94	2491.5

(1979) suggest that Carcharhinus obscurus (Lesueur, 1818), Carcharhinus brachyurus, Carcharhinus leucas (Müller & Henle, 1841), Sphyrna zygaena (Linnaeus, 1758) and Galeorhinus galeus (Linnaeus 1758) are likely to share prey species taken by A. hololepidotus and some of the other pelagic teleost carnivores. As sharks are a very important part of the upper trophic levels, the investigation of their prey in this region is clearly necessary before food resource partitioning can be more fully understood.

Of the marine mammals in this area, Sousa plumbea (Cuvier, 1829) (the humpback dolphin) occurs in shallow water. It is known to take P. olivaceum and Argyrosomus thorpei as well as other inshore species in Natal (Ross 1979, Cockroft & Ross 1983). The dolphin is likely to have the greatest dietary overlap with A. hololepidotus and, in addition, probably preys on this species in the eastern Cape.

The Indian Ocean bottlenosed dolphin, Tursiops aduncus (Ehrenberg, 1932) is the most commonly sighted and stranded cetacean on the southeast coast of South Africa (Ross 1979). It occurs in schools of up to about 2000 individuals or as few as 1-5, although they usually feed in schools of 20-50 animals (Saaman et at. 1972, Ross 1979). Ross (1979) found that the prey of bottlenose dolphins was generally smaller than 300 mm in length and included Sardinops ocellata, Merluccius capensis, Austroglossus pectoralis, Argyrosomus hololepidotus, Pomadasys olivaceum and Loligo reynaudi, clearly indicating a broad overlap of prey species with A. hololepidotus. In addition, this dolphin also preys on kob. Whether this resource sharing represents strong competition or not is unclear, as the abundance of the predators and their prey is unknown.

The Cape fur seal, Arctocephalus pusillus (Schreber. 1776) occurs commonly in the eastern Cape and has a breeding colony on Bird Island, Algoa Bay. Although its prey have not been investigated in Algoa Bay, Rand (1959) has recorded many demersal and pelagic prey including Loligo sp., Octopus sp., Sepia sp., Trachurus trachurus, Sardinops ocellata and Merluccius capensis in their diet from the west Cape coast. It seems likely that in east Cape waters this seal shares the prey of both soft bottom demersal and pelagic predators and that they also prey on A. hololepidotus.

Demersal prey

Demersal and pelagic prey species which occur over soft substrates and are taken by demersal predators in the eastern Cape are usually dark (G. feliceps) or silvery (e.g. P. olivaceum and A. hololepidotus) and may have bars (e.g. L. mormyrus). The patterns provide obliterative countershading which allows the fish to blend in with the background scattered light (Edmunds 1974, Lagler et al. 1977). The camouflage is enhanced by the fact that water is often turbid in these areas, making visual detection difficult until the final stages of attack. Consequently scent, sound and electroreception are used in turbid areas, although the sense used depends on the predator (Hobson 1963, Lissman 1963, Kalmijn 1966, Davis & Miller 1967, Hodgeson & Mathewson 1971). Solitary prey, on the other hand, may bury themselves (tonguefishes and soles) while others have strong spination (Triglidae). Although aquatic macrophytes are absent, demersal species often school near reefs where they are less threatened (Chapter 6).

Finally, changes in microhabitat may be used to reduce predation risk e.g. vertical migration by invertebrates and movement of fish schools (Clarke 1966, Hobson 1968, 1973, Hobson & Chess 1976, Major 1977, Lasiak 1982). Blaber & Blaber (1980) have noted that the effects of turbidity have not been widely investigated but that it is important to many fish, especially those which enter estuaries as juveniles.

Details on important prey taken by A. hololepidotus are described below. They appear to be associated either with soft demersal substrates or occur close to them, being important prey of demersal predators. Cheimerius nufar, although not taken by A. hololepidotus, is considered here for convenience.

Fig. 45 describes the length frequency of demersal prey taken from all predators collected during this sampling programme. The histograms therefore reflect the overall effect of predation by large top teleost carnivores. The impact of minor piscivores and of carnivores smaller than those collected here cannot be accounted for, but these figures are useful to determine the size range over which predatory teleosts interact. They also serve as a basis for comparison of the effect of other predators on the prey populations.

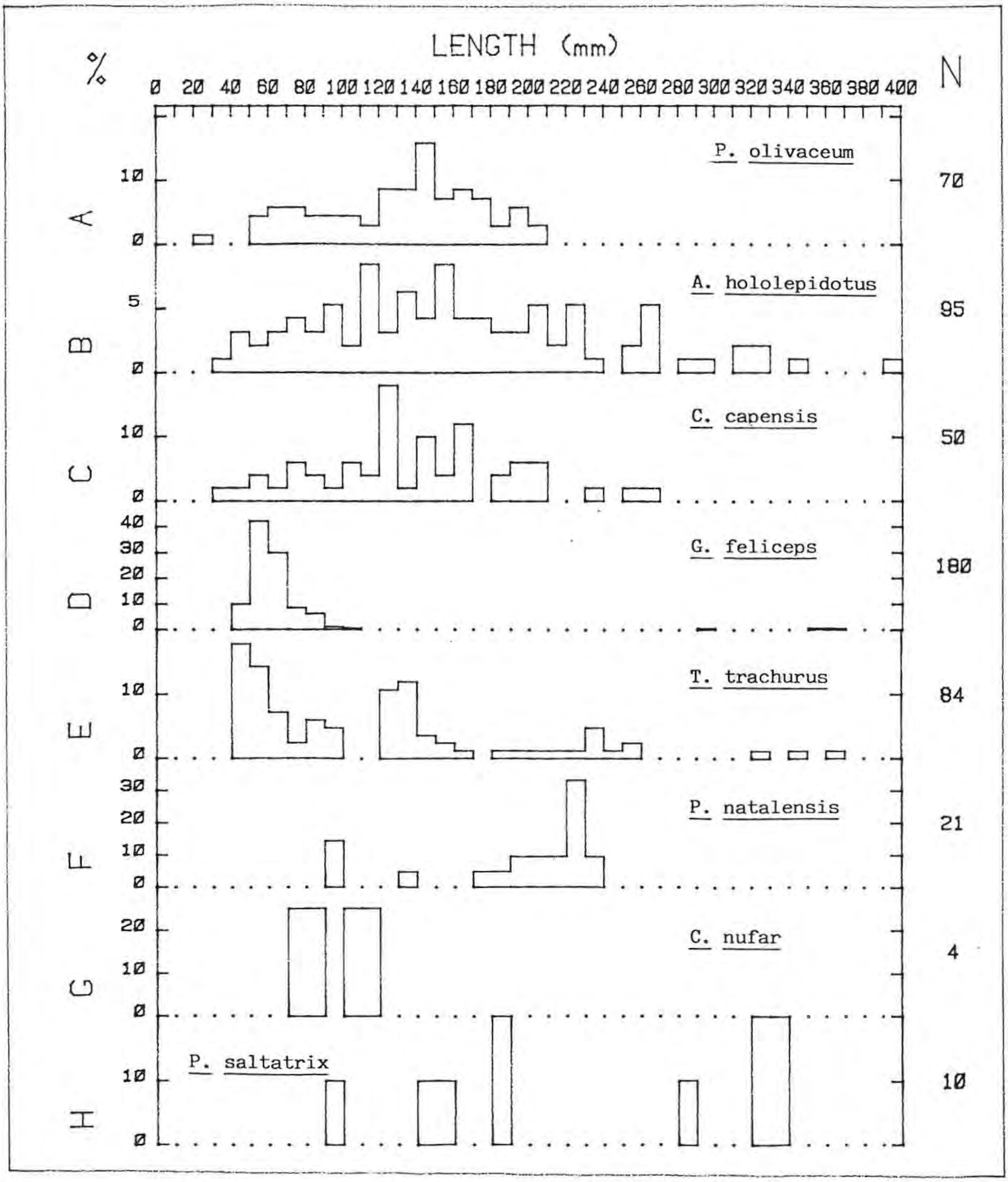


Fig. 45. Histograms of demersal and pelagic prey species taken by demersal predators. The length range of Pomadasys olivaceum (A), Argyrosomus hololepidotus (B), Cynoglossus capensis (C), Galeichthys feliceps (D), Trachurus trachurus (E), Pagellus natalensis (F), Cheimerius nufar (G) and Pomatomus saltatrix (H) are shown. One A. hololepidotus of 425 mm is not shown in (B).

Pomadasys olivaceum

P. olivaceum is an important prey species which has no current commercial importance, although in Natal it is taken by inshore anglers (Joubert 1981). In addition to its importance to all sizes of A. hololepidotus, it is taken by P. saltatrix, C. nufar, P. rupestris, L. amia, and A. aequidens, and was recorded in one T. albacares. P. olivaceum is considered by Lasiak (1982) to be planktivorous, taking Mesopedopsis slabberi, Macropetasma africanum and copepods in the surf zone of Algoa Bay. Generally similar results were obtained by Joubert & Hanekom (1980) in Natal. Buxton (in prep.) found crustaceans were the major component of their diet and mysids were most important. The length range of P. olivaceum taken during an analysis of surf zone fishes at Kings Beach, Algoa Bay, varied from 21 to 222 mm (Lasiak 1982). P. olivaceum catches made during the Thomas B. Davie cruises in the southern Cape were made up of fishes of 6 to 288 mm TL (Buxton in prep.). Teleost predators collected during this program took P. olivaceum of 28 to 209 mm TL with modes between 60 and 80 mm and 140 - 150 mm. They are similar to modes presented by Buxton (in prep.) for fish taken by trawl.

Argyrosomus hololepidotus

A. hololepidotus is an important prey species in addition to its role as a top teleost predator. It is taken by P. saltatrix, S. lalandi, A. hololepidotus, C.nufar, P. rupestris and L. amia. Those taken by carnivorous teleosts in this study were 36 - 426 mm (only those smaller than 400 mm are shown in Fig. 45). There is no clear indication of modal lengths. Smale (in prep.) found that fish of 25 to 1590 mm were caught by the Thomas B. Davie trawls. A modal size of 120 - 130 mm was found in the combined data, although the modal length varied with depth. This has been described above in regard to prey size selectivity. The size composition at two surf zone localities in Algoa Bay was between 163 and 534 mm and 148 to 452 mm. Modal lengths of 210 - 220 mm were found at Kings Beach and 270 - 280 mm at Bluewater Bay. However, the number caught was relatively low, 252 in total.

A feeding study of small kob by Smale (in prep.) has shown that A. hololepidotus smaller than 200 mm feed predominantly (>80% dry mass) on crustaceans, especially mysids. He showed, however, that those exceeding 300 mm took fish more dominantly (>60% dry mass). These findings were confirmed during the present study. Examining the length frequency taken by teleost predators it is clear that most kob were largely planktivorous (<300 mm TL), 0- year-old fish (<230 mm, Wallace & Schleyer 1979).

Cynoglossus capensis

C. capensis was taken by *P. saltatrix*, *Cheimerius nufar*, *E. guaza* but particularly by *A. hololepidotus*. The prey length varied from 38 to 262 mm, (mode 120 to 130 mm). Despite its importance to demersal fish, it has no commercial significance and is normally discarded from trawl catches, although Hecht (1976) notes that trawlers catch this species in similar quantities to *Austroglossus pectoralis*.

Galeichthys feliceps

G. feliceps was an important prey of teleost predators, especially *C. nufar* and *P. rupestris*, but particularly *A. hololepidotus*. The overall size composition varied from 45 to 365 mm (mode 50 - 60 mm). Kob only took the small size range despite a wide size range of 42 - 477 mm being found during the *Thomas B. Davie* cruise trawls (Wallace *et al*. in prep.). The reason appears to be the strong dorsal and pectoral spines which evidently protect the catfish from predation. Hoogeland *et al*. (1956) have demonstrated how a few strong spines protect sticklebacks against predation. The obvious advantages of strong spination, schooling and turbid water are optimised by adults which carry the brood in the mouth. They deposit juveniles in the shallow marine environment or in estuaries (pers.obs.) for protection.

Trachurus trachurus

T.trachurus was taken by *P. saltatrix*, *S. lalandi*, *A. hololepidotus*, *C.nufar*, *P. rupestris*, *P. praeorbitalis*, *L. amia*, *A. aequidens*, *K. pelamis* and *Thunnus albacares*. Prey size varied from 40 to 363 mm TL. The modes appear to represent 0+, 1+ and 3+ year-old fish (Geldenhuys, 1973). This species is important in the demersal and pelagic trawl catches in the western Cape (Geldenhuys 1973, Crawford 1981d) and in east Cape trawls (Hecht 1976). It is a planktivore, taking euphausids and calanoid copepods predominantly (Hecht 1976).

Pagellus natalensis

P. natalensis was taken by Pomatomus saltatrix, S. lalandi, Argyrosomus hololepidotus, L. amia and Atractoscion aequidens. The size range taken by piscivorous teleosts varied from 90 to 235 mm (mainly 220 - 230 mm). Buxton (in prep.) records that this species was more frequently trawled in Mossel Bay than in Algoa Bay and that their length ranged between 35 and 290 mm. P. natalensis preys on small fish such as Gobiidae, as well as polychaetes, small cephalopods and small crustaceans although the choice varies according to locality (Buxton in prep.).

Cheimerius nufar

C.nufar was taken by L. amia in this study. The four taken ranged between 76 and 116 mm at which size mysids and other small crustaceans form the bulk of its prey (Smale in prep.).

Pomatomus saltatrix

P. saltatrix was taken by P. saltatrix, S. lalandi, L. amia and A. hololepidotus. They varied between 99 and 340 mm TL at which size they are 0-1-year-old (van der Elst 1976). Lasiak (1982) recorded P. saltatrix of 70-508 mm in low numbers (2-9%) in the surf zone of Algoa Bay. The Thomas B. Davie trawl survey indicated that this species is very common in shallow coastal areas and Smale (in prep.) shows that trawled fish ranged between 30 and 270 mm with a mode of 130 - 140 mm FL. The infrequency of this species in the diet of piscivorous teleosts suggests they can successfully reduce predation by rapid swimming, but this needs further investigation.

In conclusion it may be seen that demersal prey are often found over sandy substrates where they obtain their food either from the benthos or the water column. They are important prey of A. hololepidotus which also takes more typically pelagic prey, such as engraulids. It is therefore clear that A. hololepidotus is a top predator of demersal food webs, although it also has a large influence on the pelagic food web.

CHAPTER 6

REEF PREDATORS

The predation of four reef predators is described. Common features of their predation strategy and their prey are discussed.

Family: Sparidae Cheimerius nufar (Ehrenberg, 1830)
Common name: Santer

Description

The body is ovate, laterally compressed and moderately deep (approx. 35% FL with dorsal spines depressed, 53% with spines erected Fig.3. The lateral line curves downwards to the caudal peduncle, which is robust and unkeeled. The caudal fin is forked. The head is bluntly conical and moderate in size (about 26.5% FL), eye is large (7.7% FL), and the mouth is terminal with 4-6 strong canines in front of each jaw. A narrow double band of villiform teeth, outer set enlarged, occurs on each jaw. The gape is largely, about 10-14% FL. The maxilla extends to below the anterior part of the eye. There are about 15 slender, elongate gill-rakers on the first gill arch. The colour is either pale pink over the entire body or six pale bars alternate with dark red vertical bands. The trailing edge of the caudal fin is black. A reddish blotch occurs at the base of the last dorsal ray. C. nufar attains 7 kg and 80 cm FL in South Africa (van der Elst 1981).

Distribution

Occurs from the south Cape coast along the entire east coast of Africa, including Madagascar, as well as in the north Indian Ocean and north-east Pacific Ocean from Malaysia to China (van der Elst 1981).

Habitat

C. nufar occurs as deep as 80 m, although it favours waters of 10-30 m in the eastern Cape. It is found in fairly large numbers over reefs, but not normally in cohesive schools. It is common in Algoa Bay and environs, and is also found west of this area to at least Mossel Bay, although it is rarely seen in the Tsitsikamma National Park. Large specimens also occur over sandy areas and are sometimes caught in association with A. hololepidotus. In Algoa Bay C. nufar of 100 - 300 mm FL are common over most shallow reefs throughout the bay. Larger specimens are frequently caught near St Croix Island and the Sundays River mouth area, where extensive broken reefs are common.

Material

A total of 3235 C. nufar were sampled in the eastern Cape between 1978 and 1982 (Fig. 46A). Of these 92.6% had either regurgitated stomach contents during capture, had empty stomachs or had been gutted. Two hundred and forty stomachs contained prey (Fig 46B). Of these, eight were shot by speargun, three were netted during gill-net trials and the rest, 229, were caught by hook and line. The stomach contents were similar, irrespective of fishing method, when predator size was taken into account. The smallest fish collected with stomach contents was 103 mm, the largest 641 mm FL. The highest stomach fullness was 7.9% of body mass, and the highest reconstituted stomach mass was 42.9%. This high value was probably caused by the retention of squid beaks in the stomach.

Feeding

The prey of C. nufar is shown in Table 23, grouped according to predator size. The principal prey are illustrated in Fig.47. The smallest group comprises eight fish between 100 and 200 mm. Invertebrates comprise the bulk of the sample both numerically (97%) and by mass (86%). Crustaceans made up the bulk of the numbers (96%) but only made up 23% by mass. Mysids were the single most important prey group, occurring in 63% of stomachs with contents, representing 83% by number and 10% by mass. Octopus vulgaris was the dominant prey species (63%) by mass, although only one was found (1%N). Fish prey were all demersal reef or ubiquitous species such as Chirodactylus brachydactylus, gobies and gobiesocids (clingfishes), which made up 3% by number and 14% by mass.

The 201 - 400 mm group took large numbers of crustaceans (81%N) which constituted 5% of the total mass. Mysids made up 80% of the number but 1% of the mass, whereas cephalopods made up 2% by number and 43% by mass

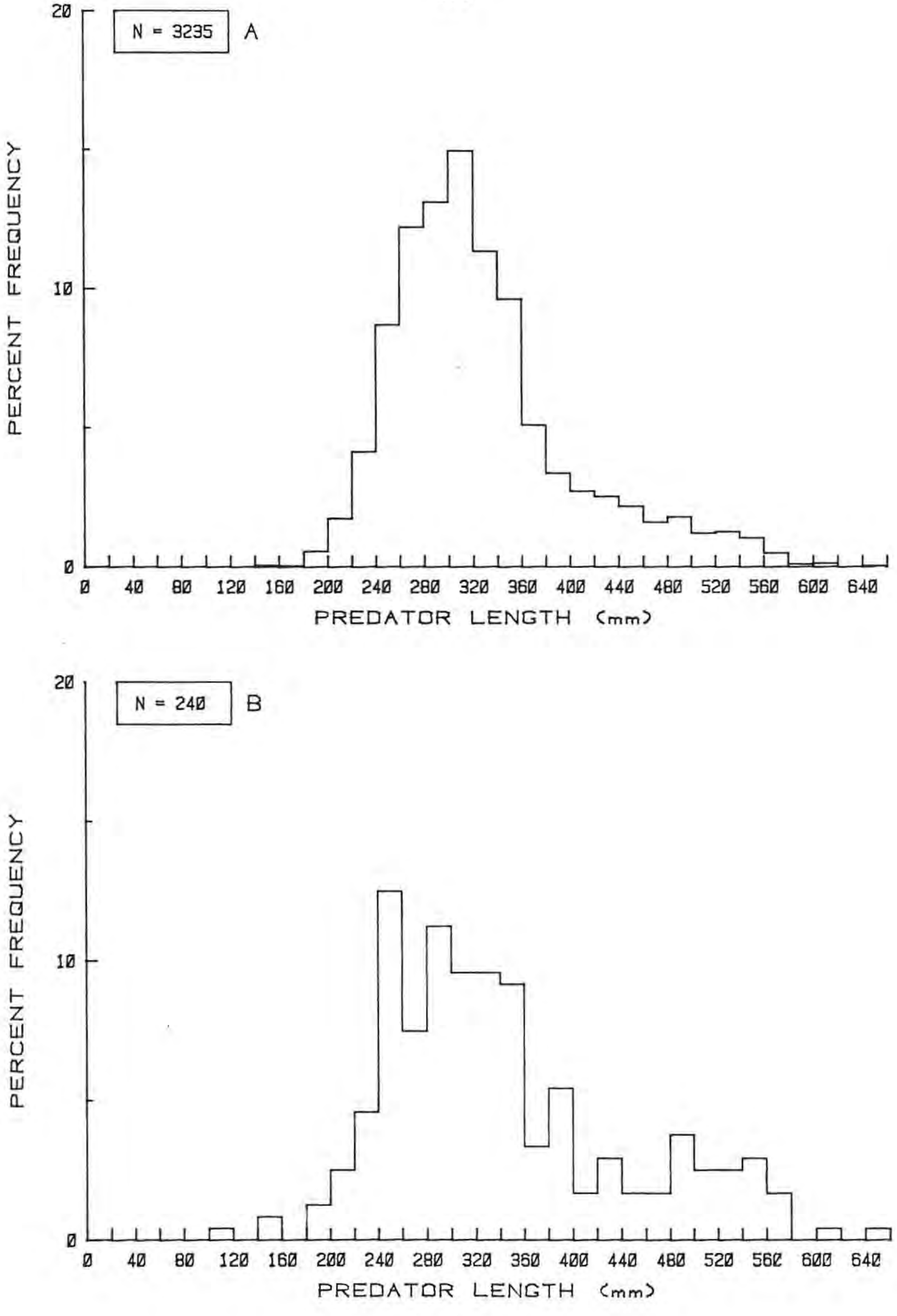


Fig. 46. Histograms of the total sample of Cheimerius nufar (A) and those with stomach contents (B).

Table 23. The prey of Cheimerius nufar, according to size.
The totals are number of stomachs (F), number of items (N) and prey wet mass (M),g.

	100 - 200 mm			201 - 400 mm			401 - 700 mm			Total		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
POLYCHAETA				0.6	0.1	<0.1				0.4	<0.1	<0.1
CRUSTACEA												
Unidentified crustaceans				0.6	0.1	<0.1	7.5	4.5	1.0	2.1	0.3	0.7
Mysidacea	50.0	69.6	8.6	10.1	78.9	1.3				9.2	75.0	0.4
Mesopedopsis slabberi				0.6	0.8	<0.1				0.4	0.7	<0.1
Mysidopsis sp.	12.5	13.0	1.1							0.4	0.8	<0.1
Caridea				0.6	0.2	0.3				0.4	0.2	<0.1
Penaeidea	12.5	0.7	12.0	1.1	0.1	0.2				1.3	0.1	0.1
Macropatasma africanum	12.5	12.3	0.6							0.4	0.8	<0.1
Brachyura	12.5	0.7	0.9	7.8	0.8	2.3	1.9	1.1	0.2	6.7	0.8	0.8
Plagusia chabrus				2.8	0.2	1.2				2.1	0.2	0.3
MOLLUSCA												
Sepiidae				1.1	0.1	0.1	1.9	1.1	0.1	1.3	0.1	0.1
Loliginidae				0.6	0.1	<0.1				0.4	<0.1	<0.1
Loligo reynaudi				10.1	1.0	32.6	5.7	3.4	4.3	8.8	1.0	12.5
Octopoda (Benthic)				1.1	0.1	0.4				0.8	0.1	0.1
Octopus vulgaris	12.5	0.7	62.7	3.9	0.4	9.9				3.3	0.4	3.1
OPHIUROIDEA				0.6	0.1	<0.1				0.4	<0.1	<0.1
OSTEICHTHYES												
Unidentified fish	12.5	0.7	1.5	19.0	2.8	7.2	7.5	4.5	0.4	16.3	2.7	2.3
Gonorynchus gonorynchus				1.1	0.1	0.4				0.8	0.1	0.1
Etrumeus teres				5.0	1.1	0.9				3.8	1.0	0.3
Sardinops ocellata				2.8	0.5	4.7	56.6	65.9	81.3	14.6	3.1	58.8
Engraulis capensis				16.2	4.3	6.5				12.1	3.8	1.9
Galeichthys feliceps				2.8	0.5	0.9				2.1	0.4	0.2
Halidesmus scapularis				1.1	0.1	0.3				0.8	0.1	0.1
Bothidae				0.6	0.1	<0.1				0.4	0.1	<0.1
Cynoglossus capensis				1.1	0.1	0.8				0.8	0.1	0.2
Cynoglossus zanzibarensis				0.6	0.1	0.4				0.4	<0.1	0.1
Cheilodactylus fasciatus				1.1	0.1	1.5				0.8	0.1	0.4
Cheilodactylus pixi				2.8	0.3	1.9	1.9	1.1	0.5	2.5	0.3	0.9
Chirodactylus brachydactylus	12.5	0.7	9.7	2.2	0.3	0.9				2.1	0.3	0.3
Acanthistius sebastoides				0.6	0.1	0.5				0.4	<0.1	0.1
Trachurus trachurus				1.7	0.2	0.9				1.3	0.2	0.3
Argyrosomus hololepidotus				0.6	0.1	2.4	5.7	3.4	3.8	1.7	0.2	3.4
Pomadasys olivaceum				0.6	0.1	0.3	5.7	3.4	4.9	1.7	0.2	3.5
Sparidae				1.1	0.2	0.1				0.8	0.2	<0.1
Boopsoidea inornata				0.6	0.1	0.1				0.4	<0.1	<0.1
Diplodus sargus				1.1	0.1	0.1				0.8	0.1	<0.1
Sarpa salpa							3.8	2.3	2.3	0.8	0.1	1.7
Spondyliosoma emarginatum				0.6	0.1	4.5	1.9	4.5	1.1	0.8	0.2	2.1
Sphyraena africanum				0.6	0.1	0.1				0.4	<0.1	<0.1
Gobiidae	12.5	0.7	1.2	9.5	1.2	2.1				7.5	1.1	0.6
Clinidae				18.4	3.7	9.3	1.9	1.1	<0.1	14.2	3.3	2.7
Pavoclinus spp.				1.1	0.1	0.3				0.8	0.1	0.1
Pavoclinus laurentii				0.6	0.1	0.3				0.4	<0.1	0.1
Cremnochorites capensis				1.7	0.6	1.3	1.9	3.4	0.2	1.7	0.7	0.5
Coccotropsis gymnoderma				1.1	0.1	0.1				0.8	0.1	<0.1
Triglidae				0.6	0.1	2.3				0.4	0.1	0.7
Gobiesocidae	12.5	0.7	1.7	1.1	0.1	<0.1				1.3	0.1	<0.1
Chatrabus melanurus				0.6	0.1	0.3				0.4	<0.1	0.1
Totals	8	138	10.8	179	1907	909.5	53	88	2208.4	240	2133	3128.8

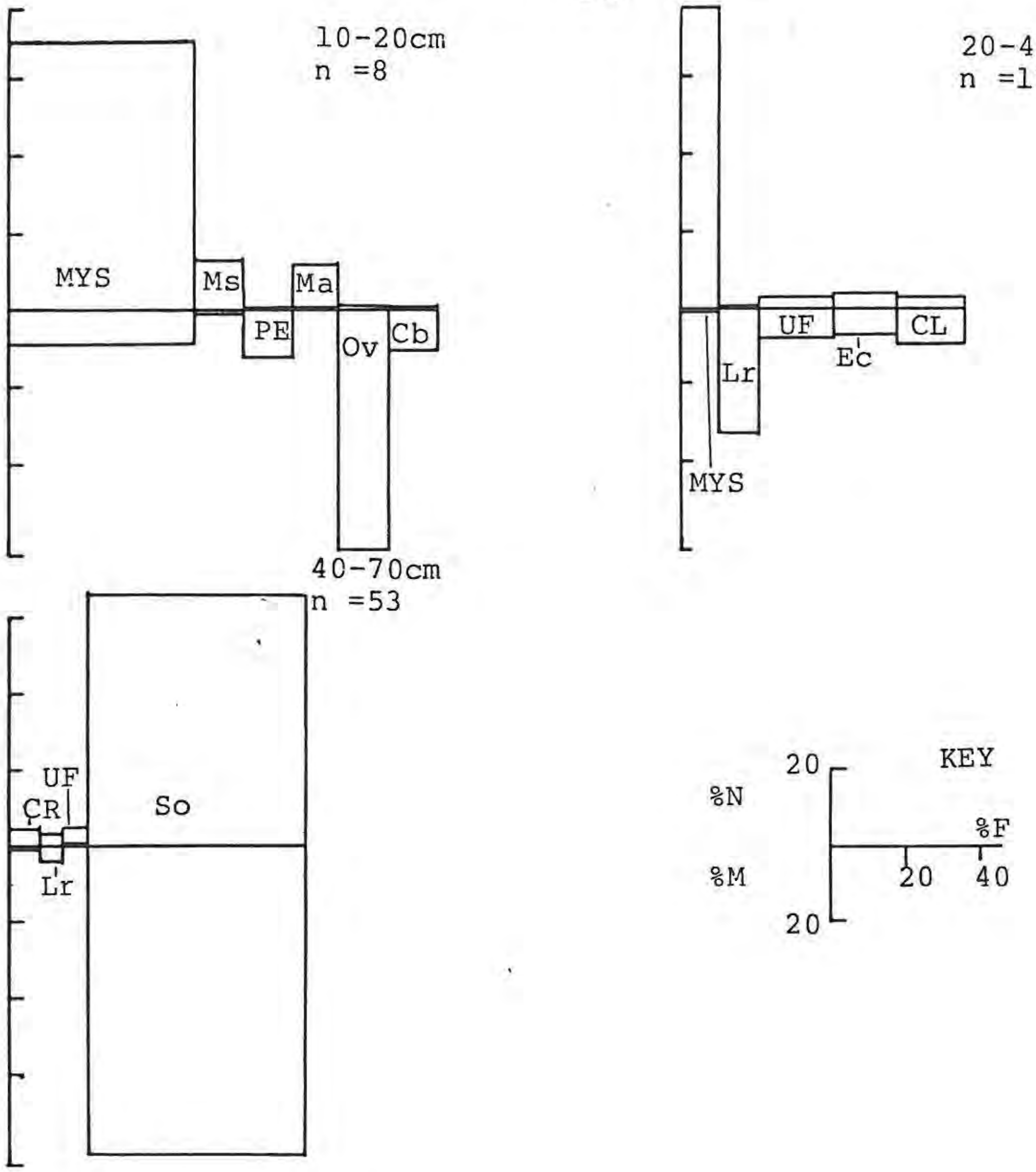


Fig. 47. Principal prey of *Cheimerius nufar.*

Cb:*Chirodactylus brachydactylus* CL:Clinidae CR:Crustacea Ec:*Engraulis capensis* Lr:*Loligo reynaudi* Ma:*Macropatasma africanum* Ms:*Mysidopsis* sp. MYS:Mysidacea Ov:*Octopus vulgaris* PE:Penaeidea So:*Sardinops ocellata* UF:Unidentified fish

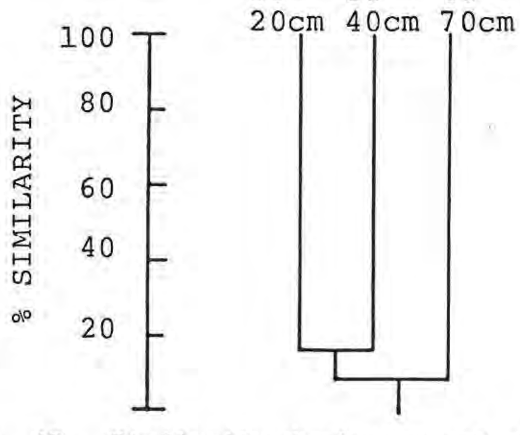


Fig. 48. Similarity dendrogram of diets of *Cheimerius nufar* size groups, according to prey mass.

taken. *L. reynaudi* was the single most important species by mass (33%) although numerically minor (1%). *O. vulgaris* was also an important prey, making up 10% by mass but only 0.4% of the numbers. In all, invertebrates made up 83% of the number and 48% of the mass of prey. Thirty-one fish taxa made up 18% by number and 52% by mass of the prey taken. These included schooling pelagic species such as *Etrumeus teres*, *S. ocellata* and *Engraulis capensis* (6%N, 13%M) and demersal and benthic fishes, such as *Gonorhynchus gonorhynchus*, *C. capensis*, *A. hololepidotus* and clinids (9%N, 31%M). *E. capensis* and Clinidae were the two most important taxa by mass.

Large *C. nufar* (401 - 700 mm) took few invertebrates (10%N, 6%M). Crustaceans made up 6% of the number and 1% of prey mass, whereas cephalopods made up 5% by number and 4% by mass. Fish made up the bulk of the prey taken (90%N, 95%M). Pelagic schooling species, *S ocellata*, (66%N, 81%M) and demersal species, such as *C. pixi* and *P. olivaceum* (19%N, 13%M), were also found. It is important to note that the majority of stomachs of this size group were obtained in 1978 when *S. ocellata* was particularly abundant in Algoa Bay. Consequently the real importance of *S. ocellata* overall may be over-emphasized.

The dietary similarity between the groups is shown in Fig.48 acording to prey mass. The 100 - 200 mm and 201 - 400 mm are 16% similar. The 401 - 700 mm groups are 8% similar to this pair.

Predator-prey length relationships

The relationship between *C. nufar* and prey length is presented for all species in Fig. 49. A minimum of 6.3% and a maximum of 84% was found for all species excluding mysids. Taking mysids into account the lower limit drops to 0.3%. An increase in the maximum size of prey taken is evident from Fig. 49, as is the increase in minimum size of prey taken. The rapid rate of increase in maximum prey size in predators below 330 mm is reduced in larger fish.

Prey size overlap is evident in Fig. 49. Species taken by *C. nufar*, of 400 mm or >400 mm are shown in Fig. 50. There is complete overlap in the size of *L. reynaudi* and *Cremnochorites capensis* taken by the two size groups of *Cheimerius nufar*. Despite the small sample available for

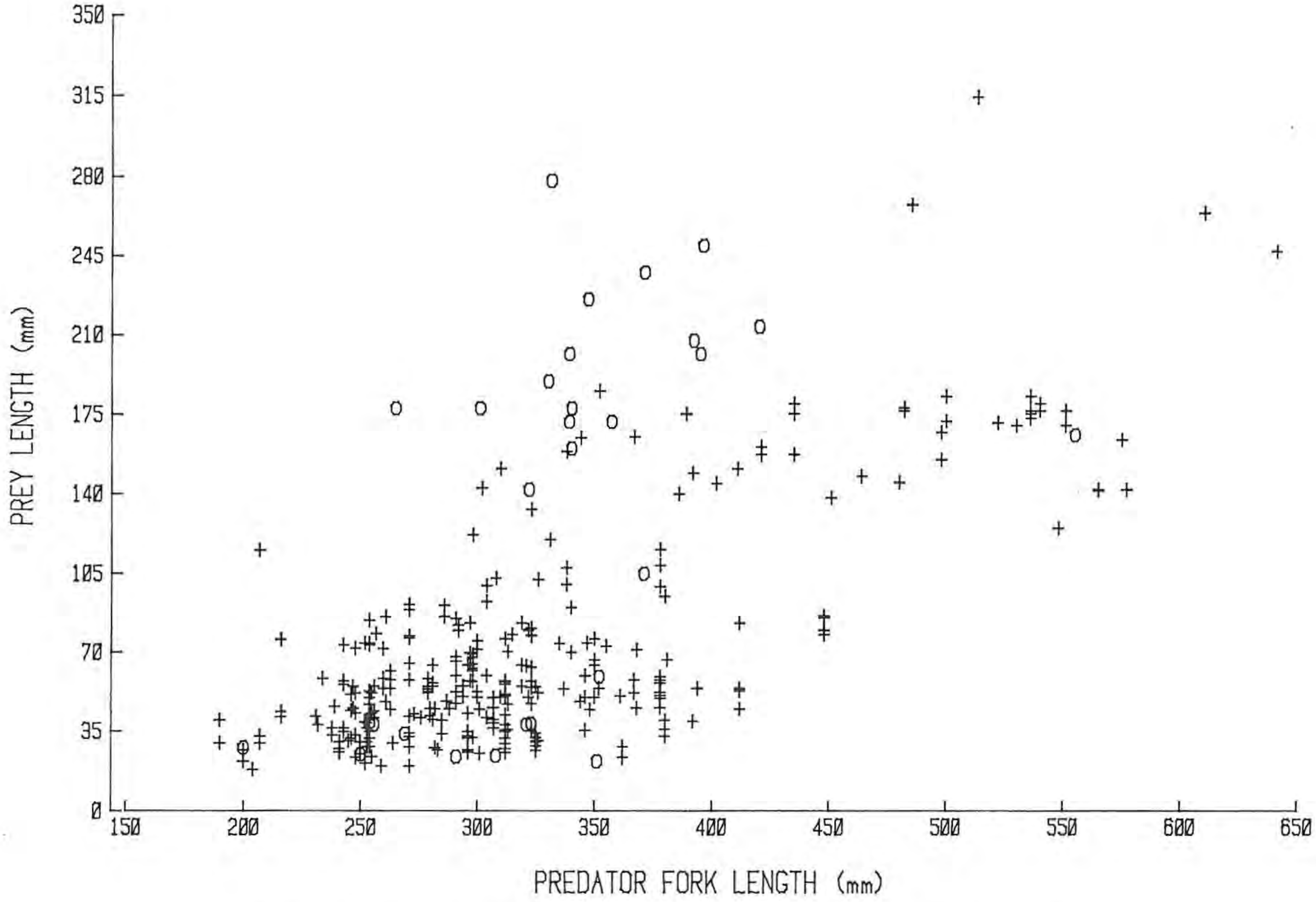


Fig. 49. Scatter diagram of prey length against fork length of <u>Cheimerius nufar</u>. Cephalopods are shown by circles and fishes by crosses.

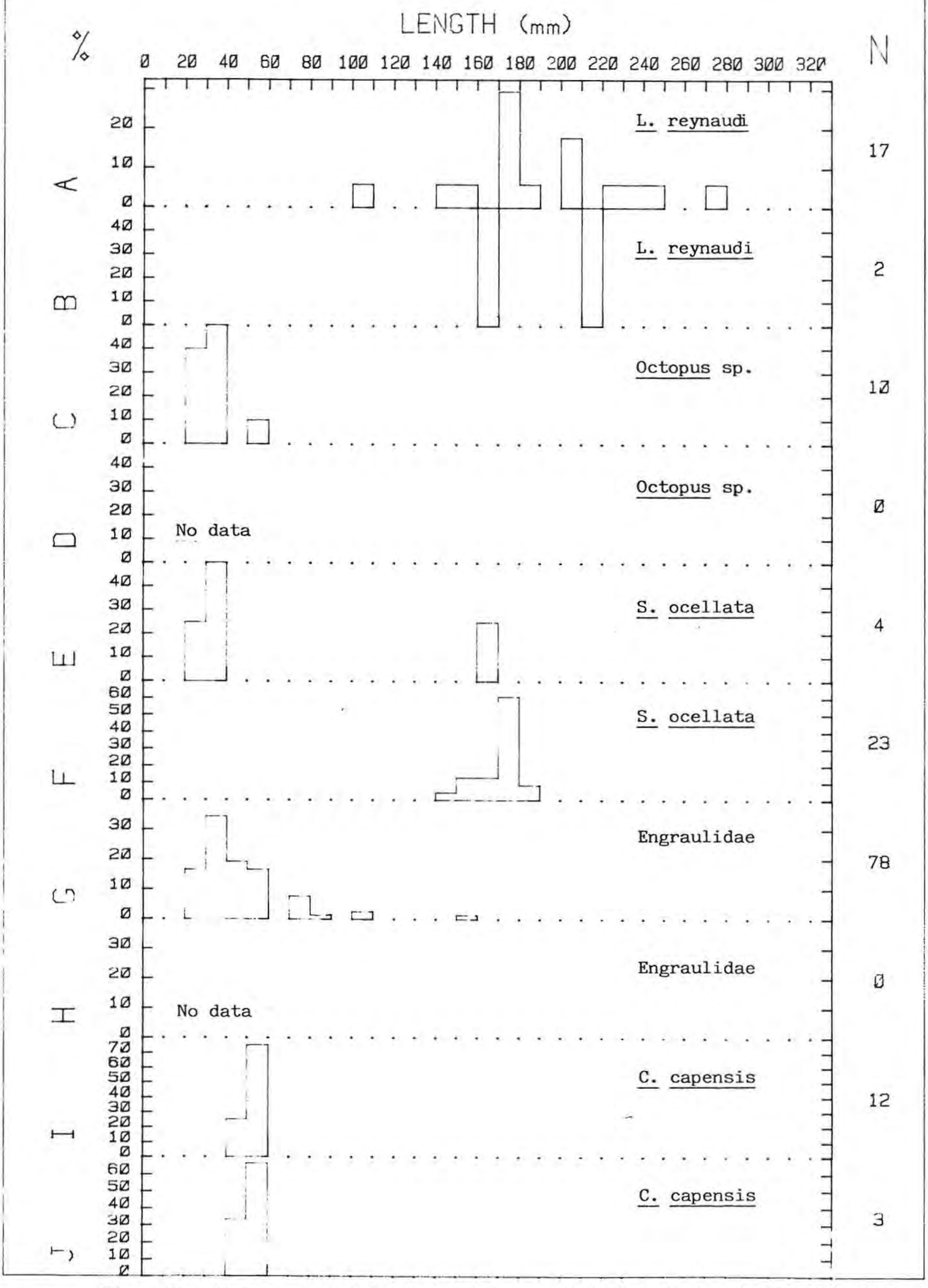


Fig. 50. Common prey of Cheimerius nufar of < 400mm (A,C,E,G,I) and > 400mm (B,D,F,H,J). Loligo reynaudi (A,B); Octopus sp. (C,D); Sardinops ocellata (E,F); Engraulidae (G,H) and Cremnochorites capensis (I,J).

comparison, small fishes appear to dominate the diet of the small size-groups. Other prey taken by C. nufar but not shown in Fig. 50 include A. hololepidotus (158 - 315 mm TL); P. olivaceum (54 - 146 mm); clinids (20 - 116 mm) G. feliceps (51 - 72 mm).

Seasonality of prey selected

As similar demersal and pelagic prey species were recorded from fish between 201 and 700 mm, they were combined in Table 24 to investigate temporal variation. Prey varied considerably through the year, schooling fishes and squid becoming sporadically important at the beginning and end of the year, while demersal reef fish such as clinids and gobies occurred almost throughout the year. From this it would appear that C. nufar is an opportunistic top predator which switches prey according to its relative abundance. When schooling species become available, especially in summer, they switch from benthic and demersal prey, to the schooling pelagic species.

Annual variation

Table 25 presents the variation of prey taken by C. nufar of 201 to 700 mm in different years. Limited data (N=26) were collected after 1980, consequently the data are combined. The importance of most of the invertebrates remained similar each year. Etrumeus teres was collected only after 1978 but S. ocellata changed from being the principal prey by mass in 1978 (84%) to a minor prey in subsequent years. This change suggests a varying relative abundance of schooling prey in different years. Engraulis capensis was only recorded after 1979. Minor species fluctuate in abundance, occasionally being absent, but this is almost certainly caused by the small sample available; more important species, such as clinids and gobies, were recorded throughout the sampling period.

Behaviour

During this study underwater observations were made of fish in their natural habitat. In addition several C. nufar were kept in the Port Elizabeth Oceanarium main display tank, where they lived with over 10 other common species of a wide size range.

In the wild

Fish of 150 - 300 mm usually occur in loose aggregations over low to moderate profile reefs (0.2 - 3 m high), or swim along the sandy bottom

Table 24. The prey of Cheimerius nufar of 201 - 700 mm taken in bi-monthly periods.
The totals are number of stomach (F), number of items (N) and prey wet mass (M),g.

Prey	January-February			March-April			May-June			July-August			September-October			November-December		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
POLYCHAETA													12.5	7.7	5.8			
CRUSTACEA Unidentified crustaceans				3.4	0.4	0.9	4.3	2.2	0.5	20.0	11.1	0.4						
Mysidacea	7.0	66.1	0.8	12.6	80.4	0.2										6.1	80.0	1.7
Mesopedopsis slabberi				1.1	1.8	<0.1												
Caridea							4.3	8.7	1.2									
Penaeidea	2.3	0.4	0.6													1.5	0.1	0.1
Brachyura	14.0	2.9	6.4	4.6	0.5	0.1							12.5	7.7	1.9	6.1	0.5	2.6
Plagusia chabrus	7.0	1.2	4.7				4.3	2.2	0.5							1.5	0.1	0.3
MOLLUSCA																		
Sepiidae	2.3	0.4	0.1				4.3	2.2	0.9				12.5	7.7	6.5			
Loliginidae	2.3	0.4	<0.1															
Loligo reynaudi	14.0	2.5	43.7	4.6	0.5	3.8				20.0	5.6	77.4	12.5	7.7	3.2	13.6	1.2	41.2
Octopoda (Benthic)	2.3	0.4	1.1													1.5	0.1	0.5
Octopus vulgaris				2.3	0.2	2.2	13.0	6.5	15.2	20.0	5.6	5.8				1.5	0.1	1.3
OPHIUROIDEA													12.5	7.7	1.9			
OSTEICHTHYES Unidentified fish	20.9	4.1	3.3	9.2	1.0	0.7	43.5	34.8	22.5	20.0	44.4	2.7	12.5	15.4	4.5	13.6	1.5	1.0
Gonorynchus gonorynchus							4.3	2.2	1.0							1.5	0.1	0.4
Etrumeus teres	4.7	1.7	0.6													10.6	2.0	1.9
Sardinops ocellata	2.3	0.4	5.4	37.9	7.6	81.3										1.5	0.4	0.2
Engraulis capensis	2.3	0.8	0.5	8.0	2.7	0.8	8.7	8.7	3.7							28.8	6.3	8.5
Galeichthys feliceps	4.7	0.8	1.4													4.5	0.8	1.3
Halidesmus scapularis	2.3	0.4	1.6	1.1	0.1	<0.1												
Bothidae																1.5	0.2	0.1
Cynoglossus capensis				1.1	0.1	0.3										1.5	0.1	0.1
Cynoglossus zanzibarensis																1.5	0.1	1.0
Cheilodactylus fasciatus							4.3	2.2	4.4							1.5	0.1	1.3
Cheilodactylus pixi				1.1	0.1	0.4	4.3	4.3	2.8							6.1	0.5	3.0
Chirodactylus brachydactylus																6.1	0.7	2.1
Acanthistius sebastoides													12.5	7.7	29.1			
Trachurus trachurus													12.5	7.7	25.9	3.0	0.4	1.0
Argyrosomus hololepidotus							13.0	6.5	23.3							1.5	0.1	15.3
Pomadasys olivaceum				3.4	0.4	4.8										1.5	0.1	0.6
Sparidae	2.3	0.8	0.2													1.5	0.2	0.1
Boopsoidea inornata																1.5	0.1	0.3
Diplodus sargus							8.7	4.3	0.6									
Sarpa salpa				2.3	0.2	2.3												
Spondyliosoma emarginatum				1.1	0.5	1.0	4.3	2.2	20.4									
Sphyraena africanum	2.3	0.4	0.4															
Gobiidae	9.3	1.7	1.8	9.2	1.5	0.4	4.3	2.2	0.4				12.5	7.7	3.9	4.5	0.5	1.8
Clinidae	25.6	10.0	11.4	5.7	1.9	0.6	8.7	8.7	2.4	40.0	27.8	10.3	12.5	7.7	3.2	19.7	2.5	9.2
Pavoclinus spp.																3.0	0.2	0.7
Pavoclinus laurentii										20.0	5.6	3.4						
Cremnochorites capensis	2.3	3.7	4.9										12.5	7.7	9.7	3.0	0.6	1.5
Coccotropsis gymnoderma													12.5	7.7	4.3	1.5	0.1	0.1
Triglidae	2.3	0.8	11.3															
Gobiesocidae				1.1	0.1	<0.1	4.3	2.2	0.1									
Chatrabus melanurus																1.5	0.1	0.8
Totals	43	242	185.6	87	825	2247.4	23	46	201.3	5	18	82.6	8	13	15.5	66	851	385.5

Table 25. Annual variation in prey taken by Cheimerius nufar of 201 - 700 mm. The totals are number of stomachs(F), number of items (N) and prey wet mass(M)g.

Prey	1978 %F	%N	%M	1979 %F	%N	%M	1980-82 %F	%N	%M
POLYCHAETA				1.1	0.2	0.2			
CRUSTACEA	6.3	0.5	1.0				1.3	0.3	0.1
Mysidacea	4.7	86.2	0.3	7.8	63.7	0.6	10.1	72.5	0.6
Mesopedopsis slabberi							1.3	2.3	0.1
Caridea							1.3	0.6	0.5
Penaeidea	1.6	0.1	<0.1				1.3	0.2	0.2
Brachyura	3.2	0.3	0.3	6.7	1.1	0.8	8.9	1.2	3.1
Plagusia chabrus	1.6	0.1	<0.1	3.3	0.5	1.9	1.3	0.2	0.2
MOLLUSCA									
Sepiidae				2.2	0.4	0.2	1.3	0.2	0.4
Loliginidae				1.1	0.2	<0.1			
Loligo reynaudi	7.9	0.6	7.6	10.0	1.8	26.7	8.9	1.1	21.0
Octopoda (Benthic)				1.1	0.2	0.4	1.3	0.2	0.4
Octopus vulgaris	1.6	0.1	0.4	1.1	0.2	4.5	6.3	0.8	12.7
OPHIUROIDEA				1.1	0.2	0.1			
OSTEICHTHYES Unidentified fish	11.1	0.9	1.6	20.0	4.1	6.5	16.4	4.1	1.9
Gonorynchus gonorynchus				1.1	0.2	0.3	1.3	0.2	0.4
Etrumeus teres				7.8	3.0	1.5	2.5	0.6	0.2
Sardinops ocellata	52.4	8.1	84.0	1.1	0.2	2.1	1.3	0.5	0.2
Engraulis capensis				22.2	9.9	7.5	11.4	4.0	5.0
Galeichthys feliceps	3.2	0.8	0.2	2.2	0.4	0.3	1.3	0.2	0.4
Halidesmus scapularis							2.5	0.3	0.7
Bothidae				1.1	0.4	0.1			
Cynoglossus capensis				2.2	0.4	1.6			
Cynoglossus zanzibarensis							1.3	0.2	0.8
Cheilodactylus fasciatus				1.1	0.2	1.1	1.3	0.2	1.9
Cheilodactylus pixi	1.6	0.1	0.5	4.4	0.9	3.2	1.3	0.2	0.4
Chirodactylus brachydactylus							5.1	0.9	1.7
Acanthistius sebastoides				1.1	0.2	1.0			
Trachurus trachurus				2.2	0.5	0.9	1.3	0.2	0.8
Argyrosomus hololepidotus				3.3	0.5	17.7	1.3	0.2	4.8
Pomadasys olivaceum				2.2	0.4	8.5	2.5	0.3	14.8
Sparidae				1.1	0.4	0.1	1.2	0.3	<0.1
Boopsoidea inornata							1.3	0.2	0.2
Diplodus sargus							2.5	0.3	0.3
Sarpa salpa	1.6	0.1	2.3				1.3	0.2	0.2
Spondyliosoma emarginatum							2.5	0.8	13.6
Spyraena africanum				1.1	0.2	0.1			
Gobiidae	1.6	0.3	0.2	8.9	1.6	1.9	10.1	1.7	1.4
Clinidae	9.5	1.2	1.2	20.0	6.0	7.7	12.7	4.3	4.8
Pavolcinus spp							2.5	0.3	0.6
Pavoclinus laurentii							1.3	0.2	0.6
Cremnochorites capensis	1.6	0.4	0.2	3.3	2.1	2.5			
Coccotropsis gymnoderma				1.1	0.2	0.1	1.3	0.2	0.1
Triglidae							1.3	0.3	4.4
Gobiesocidae				1.1	0.2	<0.1	1.3	0.2	0.1
Chatrabus melanurus	1.6	0.1	0.1						
Totals	63	778	2174.8	90	565	468.8	79	652	474.3

gullies which transect them. Although tens to hundreds of fish may be present, the aggregation does not appear to be orientated and most of the individuals swim around apparently uninfluenced by other conspecifics. Occasionally two or three form a small school or pack, and swim over the reef together. Observations of hunting behaviour were confined to search and chase, and no instances of successful predation were observed. This hunting behaviour was restricted to reef organisms and could be separated into the following components:

1. "Quartering" - swimming speed more or less doubles from "cruising speed" and the fish appeared more tense and alert, with eyes directed to the substrate. Initially the fish would swim approximately parallel to the reef, about 100 - 200 mm above it.
2. "Speculative dive" (Fig. 51). The predator swims rapidly at a cave or towards the surface of the reef, as if about to take a prey item, but rapidly decelerates, stopping about 1/3 of a body length away from the reef. It then remains immobile for a few seconds, the eyes fixed ahead on the reef. The author interpreted this as a behavioural ruse to alarm cryptic prey into alarm escape, whereupon they may be taken. No successful attacks were witnessed to confirm this interpretation. It is also possible that fish saw a movement on the reef and stopped to investigate it further.
3. "Hover" - the fish would search the reef while hovering over it, remaining immobile from a few seconds to about a minute (Fig 51).
4. "Move off" - after an unsuccessful hunt the fish moved off fairly slowly, to accelerate and repeat the behaviour nearby. C. nufar were usually coloured plain off-white over sand, but had about five broad vertical bars across the body near reefs, although this was not a clearcut difference. The bars were seen at different times through the day.

In the aquarium

All four behavioural sequences were seen in the aquarium, but they were usually enacted over flat reefs, especially those which were mussel-covered. During the "hovering" (Fig.51) the author was able to take better note of the behaviour. The individual was observed examining the substrate, searching for prey, by moving from a distance of about 60 mm off the surface. Position was maintained by fanning the pectoral fins, and the caudal fin appeared to undulate along its length. The function

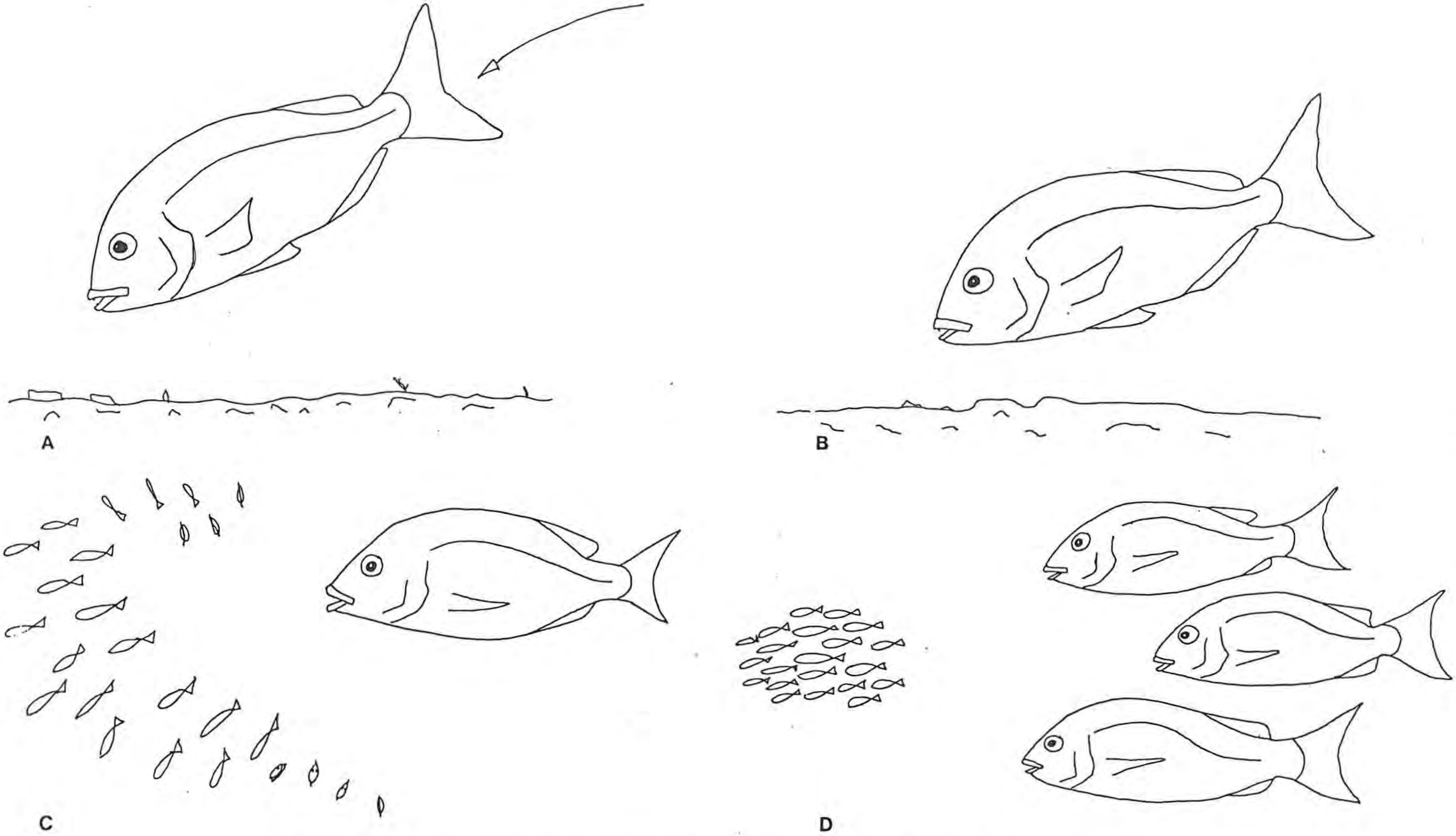


Fig. 51. Hunting behaviour of *C. nufar* A) "speculative dive", B) "hovering", C) "attack of schooled prey", D) "herding" prey.

of the dorsal and anal fins was not clear from a lateral observation point. Periodically, a dart was made to the substrate to secure a prey item.

Predation on a mixed school of juveniles (Trachurus trachurus, Sarpa salpa and Pomadasys olivaceum) was observed and the following features were noted:

1. "Cruising"- fish swam around the tank at various levels, at a relatively slow speed, showing no sign of appetitive behaviour.
2. "Approach"-the predators swim towards the school of fish at cruising speed.
3. "Feint"- the predator swims slowly towards prey which retreats. The "feint" would consist of a moderate speed charge which would not be carried through. This may have been to test for "weak" members of the school.
4. "Attack" (Fig.51)-The attack initially takes the same form as the "feint" but is more energetic. The predator swims rapidly through the school which opens up to avoid the attack. To counter this, C. nufar twists and turns rapidly, presumably chasing individual prey. The ensuing chaos prevented observation of successful attacks.
5. "Group attack"-this was essentially the same as "attack" behaviour, but was practised by 2 - 5 predators simultaneously. There was no evidence of organisation *per se*, but mutual facilitation seemed evident as the attacks appeared to be more aggressive and determined, and the skirmishes lasted longer. The school of prey was broken up more effectively as prey reacted simultaneously to several predators. This would presumably make it easier for a single susceptible prey to be picked and attacked.
6. "Herding" (Fig. 51)-this was seen on only two occasions and may be a rare occurrence. Following an intense skirmish over an artificial reef by four C. nufar, the school of prey gravitated towards the point of least attack and started to swim away. The school was very tightly packed (occupying 1/3 - 1/6 of their normal volume), swam fast and was followed by the predators, about 300 mm behind the prey. They swam around the reef (180°), were subjected to one or two further attacks after which the predators left. In the wild the school may have escaped from a high threat area to open water or possibly a cave, whichever would provide a refuge. Whether this

was in fact herding or simply the predators following prey is uncertain.

7. "Vertical chases"-these were seen when shrimps or prawns were disturbed and flicked away in escape. C. nufar responded by chasing, turning and snapping, following the course of the prey, often only catching it at the water surface.

It appears that there are two different behavioural sequences which are used to catch prey: the individual reef-oriented behaviour, and the school-oriented attack patterns. The two patterns explain how the different prey groups described below are attacked and overcome. The reactions of prey to different attack strategies will be discussed later.

Discussion

The forked tail, narrow caudal peduncle and strong canine teeth show that C. nufar is an active carnivorous fish. The deep body and well developed dorsal fin suggest that the species can manoeuvre rapidly. Such attributes are important to a predator which feeds over reefs and which chases active prey. The strong canines are important for grasping and subduing prey. The disruptive colour pattern of dark bars on a pale background probably breaks up the body shape and camouflages it over reefs and sand. Vertical bars are a common disruptive colour patter among fishes and result in effective camouflage (Cott 1957, Norman & Greenwood 1963, Edmunds 1974) especially in open water near sand.

The prey of juvenile C. nufar (78 - 150 mm) has been described by Smale (in prep.). Mysids made up 98% of prey number and 82% of prey mass. Fish contributed 0.1% by number and 6% by dry mass. These values are similar to the 100 - 200 mm group investigated here, although the invertebrates were relatively more important in the former study, probably because smaller C. nufar were examined. The mysids recorded in the former work were predominantly Gastrosaccus spp., Afromysis spp., Acanthomysis spp., Mysidopsis spp. and C. nufar juveniles are thought to capture these substrate-associated mysids (Wittmann 1977, Mauchline 1980) from reefs where they occur (Smale in prep.).

According to Coetzee & Baird (1981a), the age of the 100 - 200 mm group is about 0-1 year. The 201 - 400 mm group is between 1 and 7 years and the largest group is about 7 to 16 years. The 201 - 400 mm size group was the most numerous collected (179) and consequently a large number of prey categories were recorded from them (45). The prey included all those taken by the small group, except Mysidopsis spp. and Macropatasma africanum, although these may have been represented in the family groupings of the middle size group. Similarly the largest group (>401 mm) only had one species unrepresented in the middle size group, Sarpa salpa. Despite this overlap there was a clear trend of fish becoming more dominant and crustaceans less important, especially by mass. The largest group took Brachyura and very occasional crustaceans which were insignificant by mass (1.2%).

Coetzee & Baird's (1981a) study of 64 C. nufar stomachs collected from Algoa Bay shows a similar pattern. These authors recorded only four positively identified fish prey species (Batrichthys apiatus, Cheilodactylus fasciatus, S. ocellata and Sphyraena sp.). A large proportion of the fish (23.5%) was unidentified. Similarly, although both Loligo spp. and Octopus spp. were recorded, they were at lower percentages. These differences are probably attributable to differences in method and the use of otoliths and beaks in this study to ensure accurate prey identification. The authors also studied hindgut contents. While this may hold as an additional aid, it is clear from their results that retention of organisms with hard exoskeltons and the lack of reliably identified fish reduces the benefit of this analysis. Furthermore, it is possible that the higher incidence of crustacea in the hindgut results from the gut contents of the prey remaining in the predators' gut. The present author rejected the use of hindguts in this study as small otoliths are usually totally eroded in the stomach before passing through to the hindgut and the amorphous material which usually remains is either biased or rarely throws light on the feeding of top predatory teleosts.

The only previous study of feeding of C. nufar was that of Druzhinin (1975), who worked in the Gulf of Aden region. He found that C. nufar took no less than 10 species of fish but that the diet also included crustaceans (mantis shrimp, shrimps and crabs) and octopods. The fish he recorded included Bregmaceros, Trachurus, Carangoides, Nemipterus, Pagellus, Callyonymus, Psenopsis, Dactyloptena, Coryphaesopia and Diodon spp and Mullidae. These are representatives of both pelagic and demersal groups indicating that although the species taken is different to the local study, their niches are essentially the same.

Different hunting tactics were described earlier and these observations show that a change of behaviour is necessary to take different prey types. Individual reef hunting, individual attacks on grouped prey and "pack" hunting was described. It was observed that the latter two strategies are very similar to attacks by several other predatory species on grouped prey (e.g. Hobson 1968, Major 1978, Chapter 4) and that the prey reacted in a similar manner to those studied by these authors. The scatter diagram of prey size to predator size clearly showed a wide prey size range available to C. nufar, although the spread of the data suggests that it preys opportunistically on highly available prey as was found in the section on prey species selection. Prey of 30 to 350 mm is taken by this species although predators smaller than 200 mm have a considerably smaller maximum (about 35 mm). Predators larger than about 400 mm avoid prey smaller than about 100 mm, although this appears to be partly related to the abundance of prey. Even this size group occasionally takes small crustaceans such as crabs. Judging by the scatter diagram, potential competition between C. nufar smaller or larger than 300 mm is reduced by prey size choice, although overlap still occurs. The prey size relationship of up to 84% of predator length is surprising, considering that C. nufar does not have dentition suitable for cutting through prey. Furthermore, the large prey under consideration are L. reynaudi and A. hololepidotus. While it is possible that squid could be torn apart during a feeding frenzy, this is unlikely for large teleosts. It is possible that these large specimens were taken either as sections partially ingested by other predators such as seals or sharks or that they were taken as rejected heads of cleaned fish from anglers. The latter explanation is unlikely as kob are popular eating fish which are usually gutted but not headed at sea. However the lengths of these large fish were calculated from otolith measurements. The entire fish was not recovered from stomachs. Therefore partial ingestion is the most likely explanation for this apparent anomaly. Small fish of less than 190 mm (54%) of the predator length are more dominant and are probably close to the largest prey size normally ingested whole by C. nufar.

Stark (1970) has recorded that Lutjanus griseus take prey up to 135% of the predator length. He found that the large items that cannot be swallowed whole are shaken apart, although the majority of items are swallowed whole. Considering the similar dentition of C. nufar, this behaviour may also occur here. It is noteworthy that the prey of these two species is similar: crustaceans, fish and octopods, suggesting that they fill the same ecological niche in the different systems.

The bimonthly analysis of stomach contents showed variations which were partly a result of the varying sample size. Most material was collected from December to April. Coetzee & Baird (1981b) record a variable catch per unit effort (CPUE) from St Croix Island, Algoa Bay. In 1978 a marked peak occurred in January. The causes of these fluctuations are not clear but may well represent predators responding to patchy abundance of prey. Diving has revealed that C. nufar occurs inshore throughout the year. The importance of schooling fishes, particularly in March-April 1978, suggests that this predator responds very strongly to highly abundant prey. This probably accounts for the dominance of clupeids and engraulids from November to April, when they appear to move into the shallow coastal bay. L. reynaudi appears sporadically in the diet, perhaps coincidental with spawning activity (Chapter 4). Demersal fish make up the bulk of the prey through the rest of the year.

The peak of S. ocellata in the diet of C. nufar in 1978 and the subsequent appearance of E. capensis conforms well with data collected for the pelagic predators (see Chapter 4).

Family: Sparidae *Petrus rupestris* (Valenciennes, 1830)
Common name: red steenbras

Description

The body is laterally compressed but very robust in mature fish (Fig.3). It is moderately elongate (33% of FL with dorsal spines retracted and 39% with spines erect). The lateral line is simple, curving gently to the caudal peduncle. The caudal fin is forked and attaches to a robust caudal peduncle. The head is elongate to somewhat conical, about 30% FL and scaled to the anterior margin of the eye. The eye is about 5% FL. The mouth is terminal with powerful jaws. The gape is approximately 8 - 12% FL. The maxilla ends in front of the eye but both jaws bear powerful canines (4U, 4-6L) and teeth occur in two rows. The gill rakers are laminate in large specimens, numbering 15 - 17 in total on the outer arch (Smith 1938, Fig 25). The species attains 2 m and 50 kg (van der Elst 1981). Their colour is red-orange dorsally and laterally in small specimens with a white to cream ventral surface. A distinct large dark orange or red spot is found behind the dorsal fin. The body darkens with age, becoming copper in adults. Some, probably males, have a dark grey to black mantle dorsally. Ventrally they darken to orange or copper.

Distribution

This endemic species is found along the south and east coast of South Africa (Smith 1938).

Habitat

Found on reefs from about 10 - 100 m, *P. rupestris* is a highly prized angling and line fish which is becoming increasingly rare in popular fishing areas. However, it is still caught in large numbers on deep banks off East London and Transkei. It is caught sporadically in fair numbers off Sardinia Bay and is often seen in the Tsitsikamma National Park, where its behaviour was observed. Fish less than 600 mm FL are far more commonly seen than larger specimens while diving, possibly because bigger fish are less numerous and move offshore. They are solitary but several may occur together in the same area of reef. Their sizes may vary greatly and to date the author has not witnessed any sign of territorial aggression as suggested by van der Elst (1981). Observations to date have yet to indicate seasonal migrations of juveniles, as described by van der Elst (1981). Furthermore, although alleged to attack man in the water (Smith 1938), there have been no authenticated records since the publication of Smiths' book (Smith M.M. 1982, pers.comm. and personal research).

Material

A total of 751 P. rupestris (55 - 1310 mm FL, Fig. 52) were collected from anglers and by spearfishing and rotenone sampling. A total of 113 specimens contained stomach contents (15.1%). It was not clear whether the balance had had empty stomachs or had regurgitated their prey during capture, so they were discarded from further analyses. Those with stomach contents measured from 55 - 1186 mm FL. Seventy-eight of the fish with stomach contents were collected by line-fishing, 33 by spearfishing and two from rotenone stations. Freshly ingested prey were discounted from the latter. The prey were similar by each collection method considering size and locality and were therefore lumped for analysis. The maximum stomach fullness recorded was 5.5% and the highest reconstituted stomach fullness was 15%.

Feeding

The prey of P. rupestris is presented in Table 26 and the principal species are shown in Fig.53. One juvenile of 55 mm, collected from Tsitsikamma National Park in a rotenone station, contained 7 mysids, Mysidopsis similis (Woolridge pers.comm.), and one small, well-digested carid shrimp. M. similis is typical of reefs and sheltered caves, suggesting that predation occurs around the reef. The first record of fish in the diet is from a specimen of 190 mm which had taken three gobies.

The only invertebrate taken by P. rupestris between 201 and 400 mm was Loligo reynaudi; on one occasion it made up 3% of the number and 0.2% of the mass of prey. Fish made up the majority of the diet (98%N, 99.8%M), 80% by number and 89%M by mass being reef-associated species. Three percent by number (5%M) was made up of Trachurus trachurus, while 10% of the number and 5% of the mass was unidentified. The principal species were the fingerfins, Cheilodactylus pixi and C. fasciatus; Chirodactylus brachydactylus was less important. The Clinidae were important and one species, Clinus venustris, was positively identified from a freshly

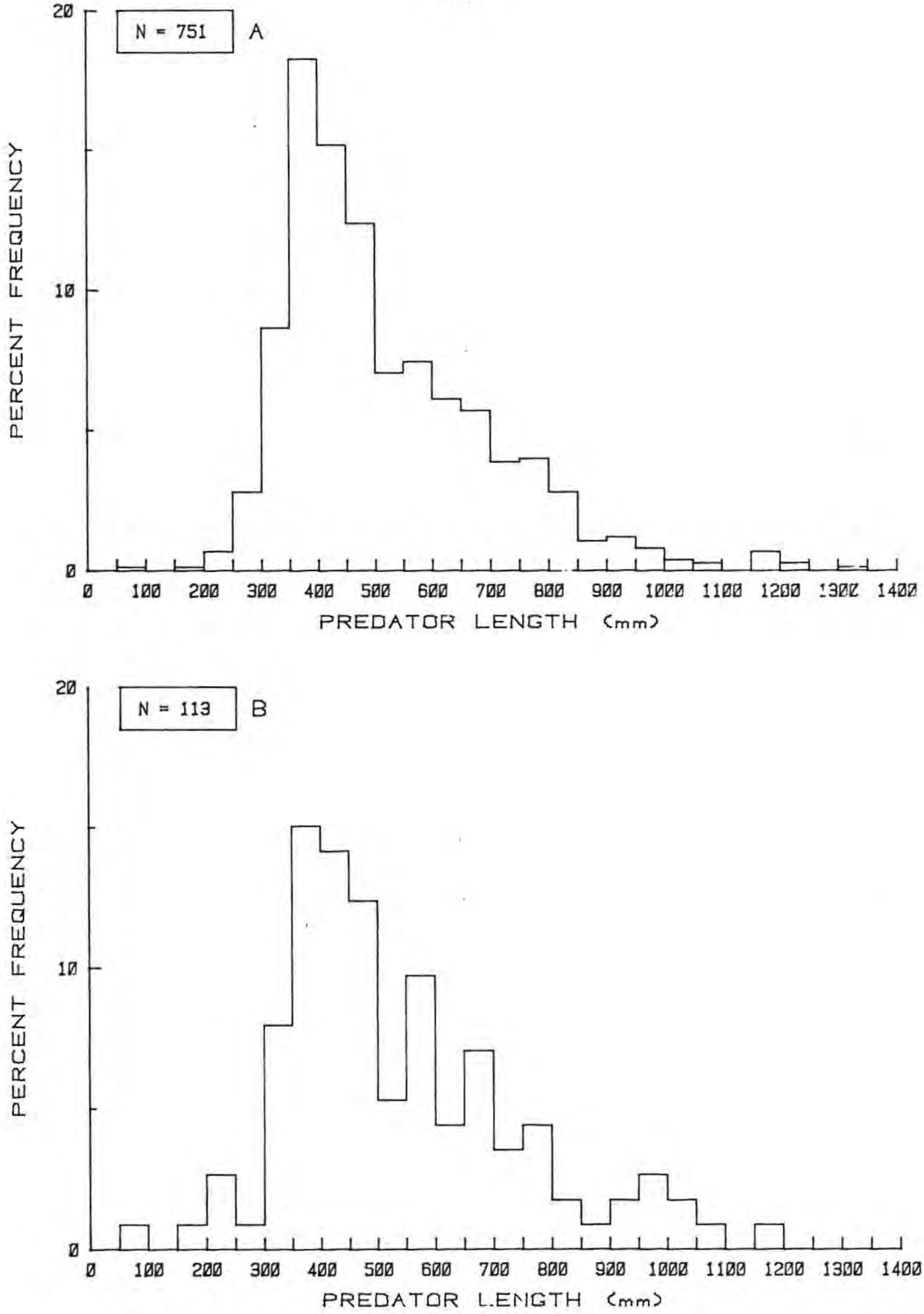


Fig. 52. Histogram of the total sample of Petrus rupestris (A) and those with stomach contents.

Table 26. The prey of *Petrus rupestris*, according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M),g.

Prey	50 - 200 mm			201 - 400 mm			401 - 700 mm			701 - 1000 mm			1001 - 1200 mm			Overall		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA																		
Mysidacea	50.0	63.6	5.6													0.9	4.4	<0.1
Caridea	50.0	9.1	1.9													0.9	0.6	<0.1
Penaeidea										5.9	3.1	0.1				0.9	0.6	<0.1
Scyllarides elisabethae										5.9	3.1	0.8				0.9	0.6	<0.2
MOLLUSCA																		
Sepiidae							1.7	1.4	0.2	5.9	3.1	0.1				1.8	1.3	0.1
Loligo reynaudi				3.2	2.5	0.2	6.8	5.7	0.4	5.9	3.1	<0.1				5.3	3.8	0.2
Octopoda (Benthic)							3.4	2.9	0.9							1.7	1.3	0.4
Octopus vulgaris							3.4	2.9	13.4	11.8	6.3	15.7				3.5	2.5	9.4
CHONDRICHTHYES																		
Haploblepharus fuscus													25.0	14.3	19.0	0.9	0.6	5.3
OSTEICHTHYES																		
Unidentified fish				12.9	10.0	5.0	8.5	7.1	0.6	35.3	18.8	11.1	25.0	14.3	0.3	14.2	10.0	3.5
Gonorynchus gonorynchus							1.7	1.4	0.7							0.9	0.6	0.3
Etrumeus teres										5.9	3.1	1.9				0.9	0.6	0.5
Galeichthyes feliceps							1.7	1.4	1.8	5.9	9.4	11.2				1.8	2.5	3.6
Genypterus capensis													50.0	28.6	22.3	1.8	1.3	6.2
Cheilodactylidae							1.7	1.4	0.2							0.9	0.6	0.1
Cheilodactylus fasciatus				19.4	15.0	36.1	10.2	8.5	5.9							10.6	7.5	4.8
Cheilodactylus pixi				25.8	22.5	20.6	5.1	5.7	1.2							9.7	8.1	1.9
Chirodactylus brachydactylus				6.5	5.0	8.8	6.8	5.7	4.4							5.3	3.8	2.4
Acanthistus sebastoides				3.2	2.5	0.7	15.3	14.3	19.0	17.7	12.5	13.9				11.5	9.4	11.2
Trachurus trachurus				3.2	2.5	4.5	1.7	1.4	4.2	5.9	9.4	10.0	25.0	14.3	18.6	3.5	3.8	9.7
Argyrosomus hololepidotus										5.9	3.1	3.4				0.9	0.6	0.9
Pomadasys olivaceum							3.4	2.9	2.2							1.8	1.3	0.9
Boopsoidea inornata				3.2	2.5	6.2	8.5	7.1	16.7	5.9	3.1	13.7				6.2	4.4	10.6
Diplodus sargus							6.8	5.7	14.3	11.8	9.4	5.9				5.3	4.4	7.2
Gymnocrotaphus curvidens													25.0	14.3	25.6	0.9	0.6	7.1
Pachymetopon aeneum				3.2	2.5	2.5	1.7	1.4	0.4				25.0	14.3	14.2	2.7	1.9	4.3
Polysteganus undulosus							1.7	1.4	0.3							0.9	0.6	0.1
Pterogymnus laniarius							3.4	2.9	1.8							1.8	1.3	0.7
Sarpa salpa				3.2	2.5	2.0	8.5	7.1	5.3							5.3	3.8	2.2
Spondyliosoma emarginatum							3.4	2.9	0.9							1.8	1.3	0.4
Gobiidae	50	27.3	92.5													0.9	1.9	<0.1
Clinidae				19.4	15.0	7.2	3.4	2.9	0.6							7.1	5.0	0.7
Clinus spp.				3.2	2.5	0.7										0.9	0.6	<0.1
Clinus superciliosus							1.7	1.4	2.2							0.9	0.6	0.9
Clinus venustris				3.2	2.5	1.8										0.9	0.6	0.1
Tripterygidae				3.2	2.5	0.5										0.9	0.6	<0.1
Cremochorites capensis				3.2	2.5	0.4										0.9	0.6	<0.1
Scopaena scrofa							1.7	1.4	0.8							0.9	0.6	0.3
Conger wilsoni										17.7	9.4	12.1				2.7	1.9	3.1
Chatrabus melanurus				9.7	7.5	2.8	3.4	2.9	1.7	5.9	3.1	<0.1				5.3	3.8	0.9
Totals	2	11	1.1	31	40	442.4	59	70	2649.2	17	32	1681.7	4	7	1828	113	160	6602.4

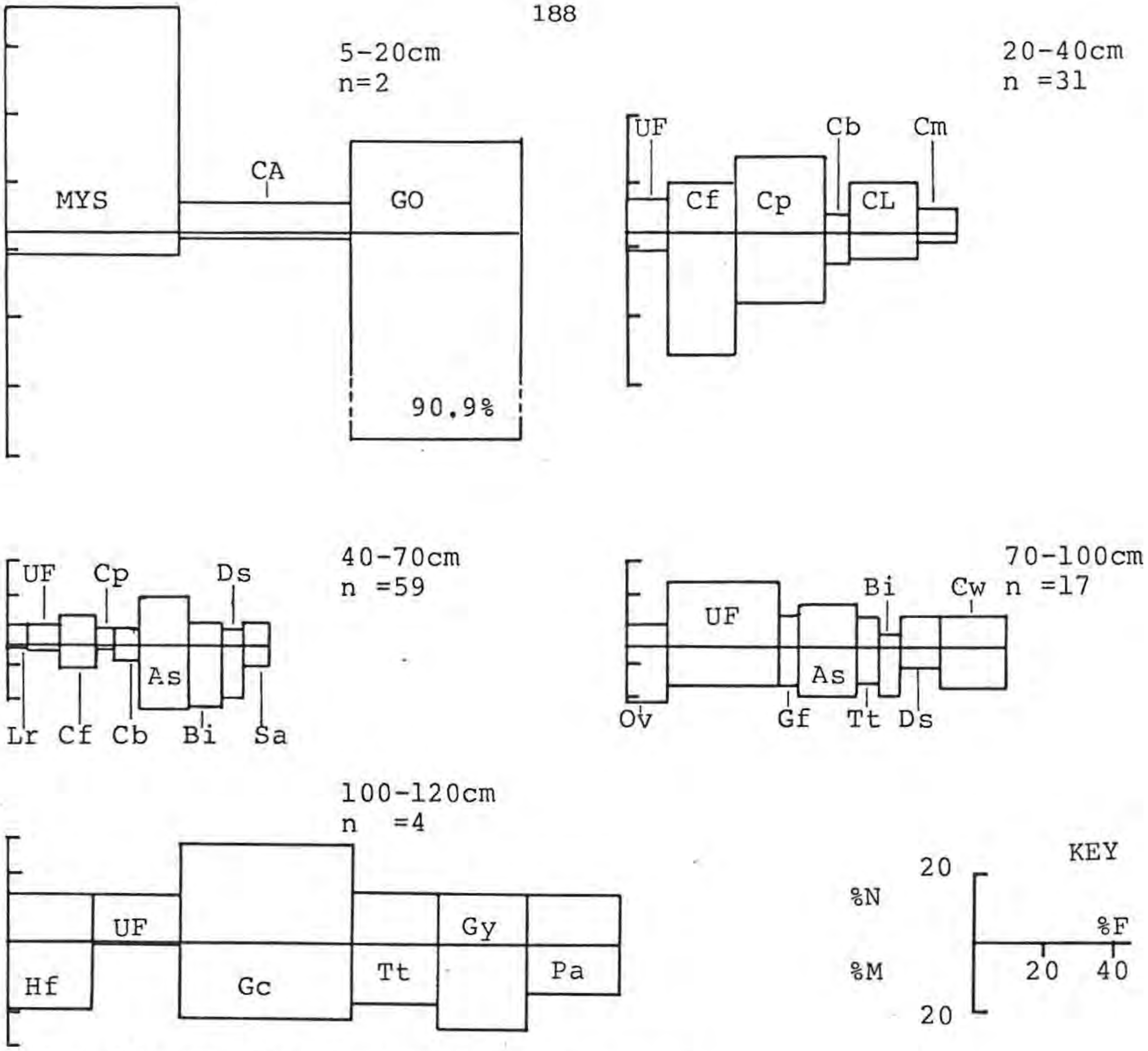


Fig. 53. Principal prey of *Petrus rupestris*.

As:*Acanthistius sebastoides* Bi:*Boopsoidea inornata* CA:Caridea
Cb:*Chirodactylus brachydactylus* Cf:*Cheilodactylus fasciatus* CL:Clinidae
Cm:*Chatrabus melanurus* Cp:*Cheilodactylus pixi* Cw:*Conger wilsoni* Ds:*Diplodus sargus*
Gc:*Genypterus capensis* Gf:*Galeichtys feliceps* GO:Gobiidae Gy:*Gymnocroptaphus curvidens*
Hf:*Haploblepharus fuscus* Lr:*Loligo reynaudi* MYS:Mysidacea Ov:*Octopus vulgaris*
Pa:*Pachymetopon aeneum* Sa:*Sarpa salpa* Tt:*Trachurus trachurus* UF:Unidentified fish

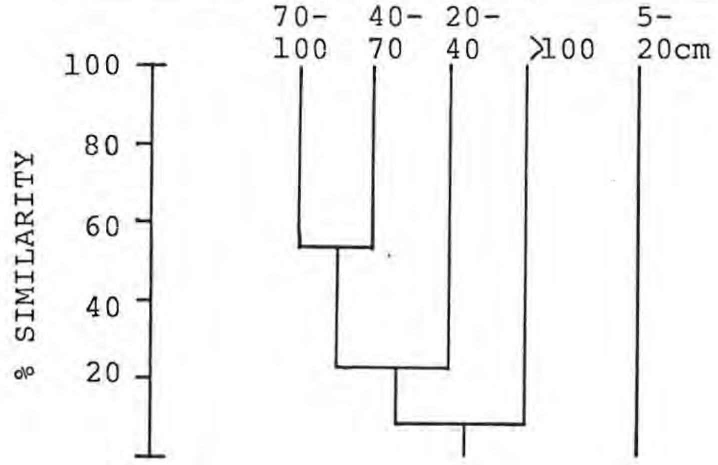


Fig. 54. Similrity dendrogram of diets of *Petrus rupestris* size groups, according to prey mass.

ingested fish. Other species taken were A. sebastoides, B. inornata, P. aeneum, S. salpa, Tripterygiidae, including Cremnochorites capensis, and the frogfish, Chatrabus melanurus.

The 401 - 700 mm group took four invertebrate groups: sepiids, L. reynaudi, unidentified benthic octopods and O. vulgaris which made up the largest mass contribution. In all, these cephalopods represented 13% of the number and 15% of the mass of prey taken. The rockcod, A. sebastoides, was the principal prey species, while the fingerfin C. fasciatus ranked second. Other principal prey species were B. inornata, D. sargus, S. salpa, C. pixi and C. brachydactylus. Reef-associated fish comprised 70% by number and 74% by mass of prey. Pomadasys olivaceum and Galeichthys feliceps, which are associated with sand areas but also occur on reefs, made up 9% by number and 7% by mass of the prey. The pelagic Trachurus trachurus was a minor item, 1% by number and 4% by mass.

The 701 - 1000 mm size group took five invertebrate prey types: prawns, S. elisabethae, sepiids, L. reynaudi and O. vulgaris. The crustaceans made up 6% by number and 1% by prey mass. Cephalopods contributed 13% by number but 16% by mass. The dominant fish prey were Acanthistius sebastoides, Conger wilsoni, T.trachurus, B. inornata and D. sargus. Others included E. teres, G. feliceps, Argyrosomus hololepidotus and Chatrabus melanurus. Reef fish accounted for 28% by number and 34% by mass of prey, demersal soft bottom or ubiquitous species made up 22% of the number and 27% of the mass taken. Pelagic prey constituted 13% by number and 12% of the mass ingested.

Four fish between 1001 and 1200 mm were collected. The catshark H. fuscus and the teleosts Genypterus capensis, T. trachurus, Gymnocrotaphus curvidens and P. aeneum made up the prey. Forty-three per cent were reef fish 29% were soft bottom-associated and 14% were pelagic. These groups represented 59%, 22% and 19% of the prey mass, respectively.

The prey of P. rupestris are primarily reef-associated and the rest are either found over sandy areas or are pelagic, but may have been close to reefs when taken. All are solitary or found in small groups except for S.

salpa, P. olivaceum, A. hololepidotus, T. trachurus, G. capensis, E. teres, L. reynaudi and mysids. With an increase in predator size the prey changes from small crustaceans such as mysids to larger invertebrates and fish. The teleosts taken are initially composed of families of small fishes such as clinids and gobies, but with growth large species are taken such as *D. sargus, H. fuscus* and *G. curvidens.* The similarity diagram of diets of the size groups of *P. rupestris* is shown in Fig. 54 according to prey mass. The 701 - 1000 mm and 401 - 700 mm are clearly most similar (54%). The 50 - 200 mm group has no prey in common with conspecifics, although the sample size is very small.

Prey selection by regions

The prey of *P. rupestris* is presented on a regional basis in Table 27. Broader size class groupings are used because, although it was shown above that there is a change of principal prey with growth, there were insufficient data to use smaller size groups in this analysis. Those collected at East London show the greatest difference in prey compared to similar sized fish elsewhere, although there is overlap with prey such as *Cheilodactylus pixi*, benthic octopods, *Conger wilsoni* and *T. melanurus*. Thus, although they are taking similar types of prey, *S. scrofa, Pterogymnus laniarius, Polysteganus undulosus* and *E. teres* are not recorded from red steenbras further south. This difference probably results from the warmer and deeper water (60 - 100 m) that characterises the fishing areas for *P. rupestris* off East London.

The prey is more similar between Algoa Bay and the south coast areas and the difference may be accounted for by sample variation. One interesting feature of the small-group fish is that the dominance of *C. pixi* and *C. fasciatus* in the diet changes between these areas. This may be attributable to distributional preferences, *C. pixi* being found in warmer waters (Smith 1980).

Predator-prey length relationships

A scatter diagram of the length of *P. rupestris* and its prey is shown in Fig. 55. There is a concomitant increase in size of prey with growth although the prey vary between 7 and 69% of predator length. Octopod mantle lengths are 7 - 13% of predator length.

Table 27 (a). The prey of *Petrus rupestris* taken off East London according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	50 - 400 mm			401 - 700 mm			701 - 1200 mm			Total		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Penaeidea							20	11.1	0.9	7.7	5.3	0.6
Syllarides elisabethae							20	11.1	6.5	7.7	5.3	4.3
MOLLUSCA												
Sepiidae				14.3	12.5	4.3				7.7	5.3	1.5
Octopoda (Benthic)				14.3	12.5	3.8				7.7	5.3	1.3
OSTEICHTHYES												
Unidentified fish	100.0	50.0	37.5	14.3	12.5	2.9	60.0	33.3	50.6	38.5	26.3	34.2
Gonorynchus gonorynchus				14.3	12.5	16.7				7.7	5.3	5.7
Etrumeus teres							20.0	11.1	16.2	7.7	5.3	10.6
Cheilodactylus pixi	100.0	50.0	62.5							7.7	5.3	0.2
Polysteganus undulosus				14.3	12.5	6.7				7.7	5.3	2.3
Pterogymnus laniarius				28.6	25.0	44.8				15.4	10.5	15.4
Scopaena scrofa				14.3	12.5	21.0				7.7	5.3	7.2
Conger wilsoni							40.0	22.2	25.7	15.4	10.5	16.8
Chatrabus melanurus							20.0	11.1	0.1	7.7	5.3	0.1
Totals	1	2	0.8	7	8	105	5	9	200.2	13	19	305.8

Table 27 (b). The prey of *Petrus rupestris* taken in Algoa Bay and environs, according to size. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	50 - 400 mm			401 - 700 mm			701 - 1300 mm			Total		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
MOLLUSCA												
Loligo reynaudi	7.7	6.3	0.9	4.5	3.8	<0.1	7.7	4.8	<0.1	6.3	4.8	<0.1
Octopus vulgaris							7.7	4.8	7.5	2.1	1.6	6.0
CHONDRICHTHYES												
Haploblepharus fuscus							7.7	4.8	11.6	2.1	1.6	9.3
OSTEICHTHYES												
Unidentified fish				9.1	7.7	0.2	30.8	19.0	3.0	12.5	9.5	2.5
Galeichthys feliceps							7.7	14.2	6.3	2.1	4.8	5.0
Genypterus capensis							15.4	9.5	13.6	4.2	3.0	10.8
Cheilodactylidae				4.5	3.8	0.9				2.1	1.6	0.2
Cheilodactylus fasciatus	7.7	6.3	1.3	9.1	7.7	11.5				6.3	4.8	2.0
Cheilodactylus pixi	30.8	25.0	71.7	9.1	11.5	1.9				12.5	11.1	2.5
Chirodactylus brachydactylus				9.1	7.7	2.4				4.2	3.2	0.4
Acanthistius sebastoides				13.6	15.4	38.6	7.7	4.8	4.7	8.3	7.9	10.4
Trachurus trachurus							7.7	4.8	11.3	2.1	1.6	9.0
Argyrosomus hololepidotus							7.7	4.8	1.9	2.1	1.6	1.5
Pomadasys olivaceum				4.5	3.8	0.9				2.1	1.6	0.1
Boopsoidea inornata				4.5	3.8	12.4	7.7	4.8	7.7	4.2	3.2	8.2
Diplodus sargus							7.7	9.5	3.1	2.1	3.2	2.5
Gymnocrotaphus curvidens							7.7	4.8	15.6	2.1	1.6	12.4
Pachymetopon aeneum	7.7	6.3	9.8	4.5	3.8	1.6	7.7	4.8	8.7	6.3	4.8	7.5
Sarpa salpa				13.6	11.5	16.9				6.3	4.8	2.9
Spondyliosoma emarginatum				9.1	7.7	3.8				4.2	3.2	0.7
Gobiidae	7.7	18.8	0.9							2.1	4.8	<0.1
Clinidae	23.1	18.8	4.4	4.5	3.8	1.8				8.3	6.3	0.4
Conger wilsoni							7.7	4.8	5.0	2.1	1.6	4.0
Chatrabus melanurus	23.1	18.8	10.9	9.1	7.7	7.1				10.4	7.9	1.5
Totals	13	16	112.4	22	26	645.1	13	21	3001.7	48	63	3759.2

Table 27 (c). The prey of *Petrus rupestris* taken from Tsitsikamma National Park and Mossel Bay. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	50 - 400 mm			401 - 700 mm			701 - 1300 mm			Total		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Mysidacea	5.3	21.2	<0.1							1.9	9.0	<0.1
Caridea	5.3	3.0	<0.1							1.9	1.3	<0.1
MOLLUSCA												
Sepiidae							33.3	11.1	0.3	1.9	1.3	<0.1
Loligo reynaudi				10.0	8.3	0.6				5.8	3.8	0.4
Octopoda (Benthic)				3.3	2.8	1.1				1.9	1.3	0.8
Octopus vulgaris				6.7	5.6	18.7	33.3	11.1	13.0	5.8	3.8	15.6
OSTEICHTHYES												
Unidentified fish	15.8	9.1	6.6	6.7	5.6	0.7				9.6	6.4	1.4
Galeichthys feliceps				3.3	2.8	2.5				1.9	1.3	1.9
Cheilodactylus fasciatus	26.3	15.2	47.8	13.3	11.1	4.3				17.3	11.5	9.5
Cheilodactylus pixi	15.8	12.1	3.0	3.3	2.8	1.1				7.7	6.4	1.2
Chirodactylus brachydactylus	10.5	6.1	11.7	6.7	5.6	5.4				7.7	5.1	5.5
Acanthistius sebastoides	5.3	3.0	1.0	20.0	16.7	13.4	66.7	33.3	30.2	17.3	12.8	13.8
Trachurus trachurus	5.3	3.0	6.1	3.3	2.8	5.8	33.3	33.3	54.9	5.8	6.4	11.8
Pomadasys olivaceum				3.3	2.8	2.7				1.9	1.3	2.0
Boopsoidea inornata	5.3	3.0	8.3	13.3	11.1	19.0				9.6	6.4	15.3
Diplodus sargus				13.3	11.1	19.9	33.3	11.1	1.6	9.6	6.4	15.1
Sarpa salpa	5.3	3.0	2.7	6.7	5.6	1.6				5.8	3.8	1.5
Clinidae	15.8	9.1	8.1	3.3	2.8	0.2				7.7	5.1	1.2
Clinus spp.	5.3	3.0	1.0							1.9	1.3	0.1
Clinus superciliosus				3.3	2.8	3.1				1.9	1.3	2.3
Clinus venustris	5.3	3.0	2.4							1.9	1.3	0.3
Tripterygiidae	5.3	3.0	0.7							1.9	1.3	0.1
Cremnochorites capensis	5.3	3.0	0.5							1.9	1.3	0.1
Totals	19	33	330.3	30	36	1899.1	3	9	308	52	78	2537.4

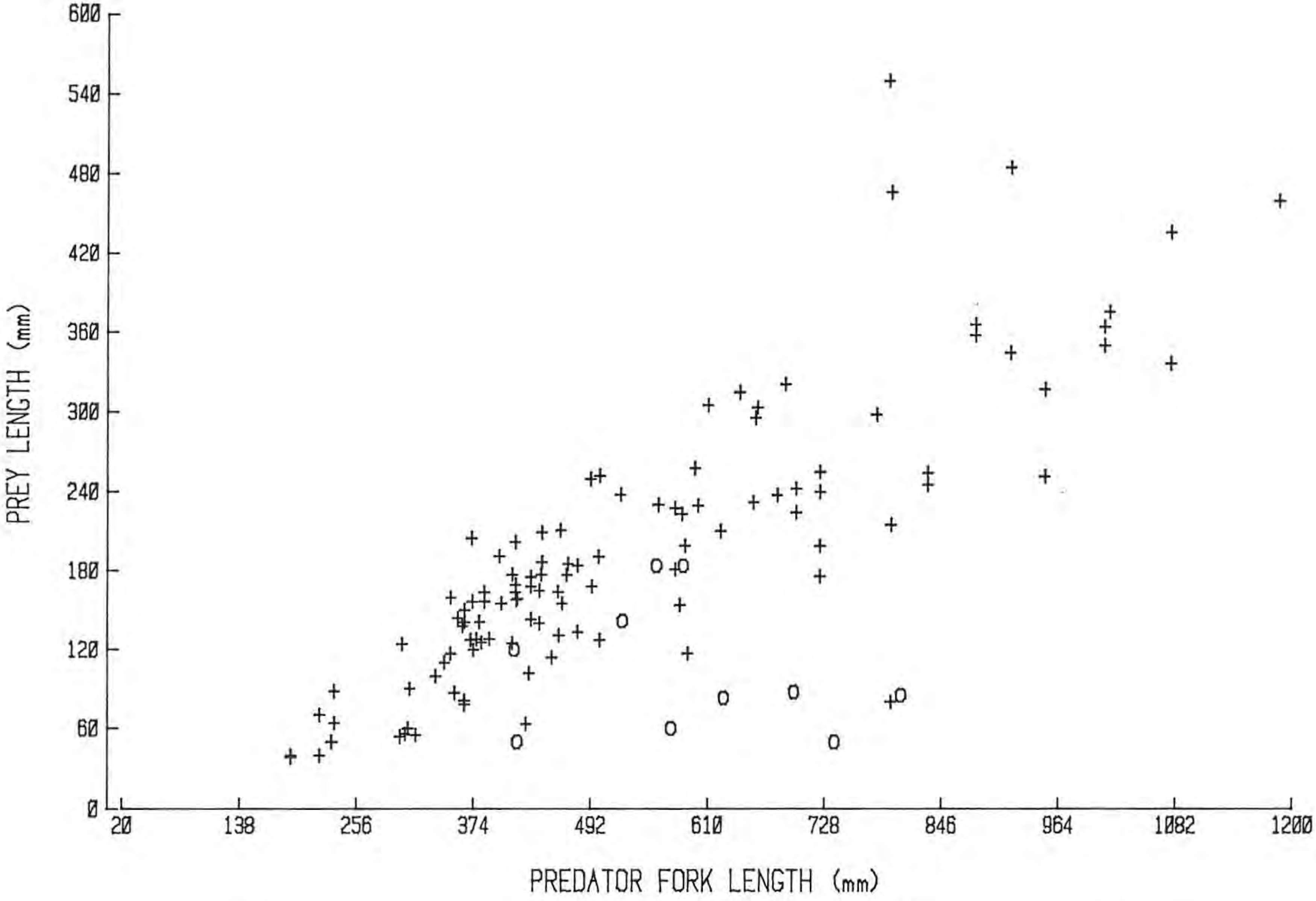


Fig. 55. Scatter diagram of prey length against fork length of Petrus rupestris Cephalopods are shown by circles and fishes by crosses.

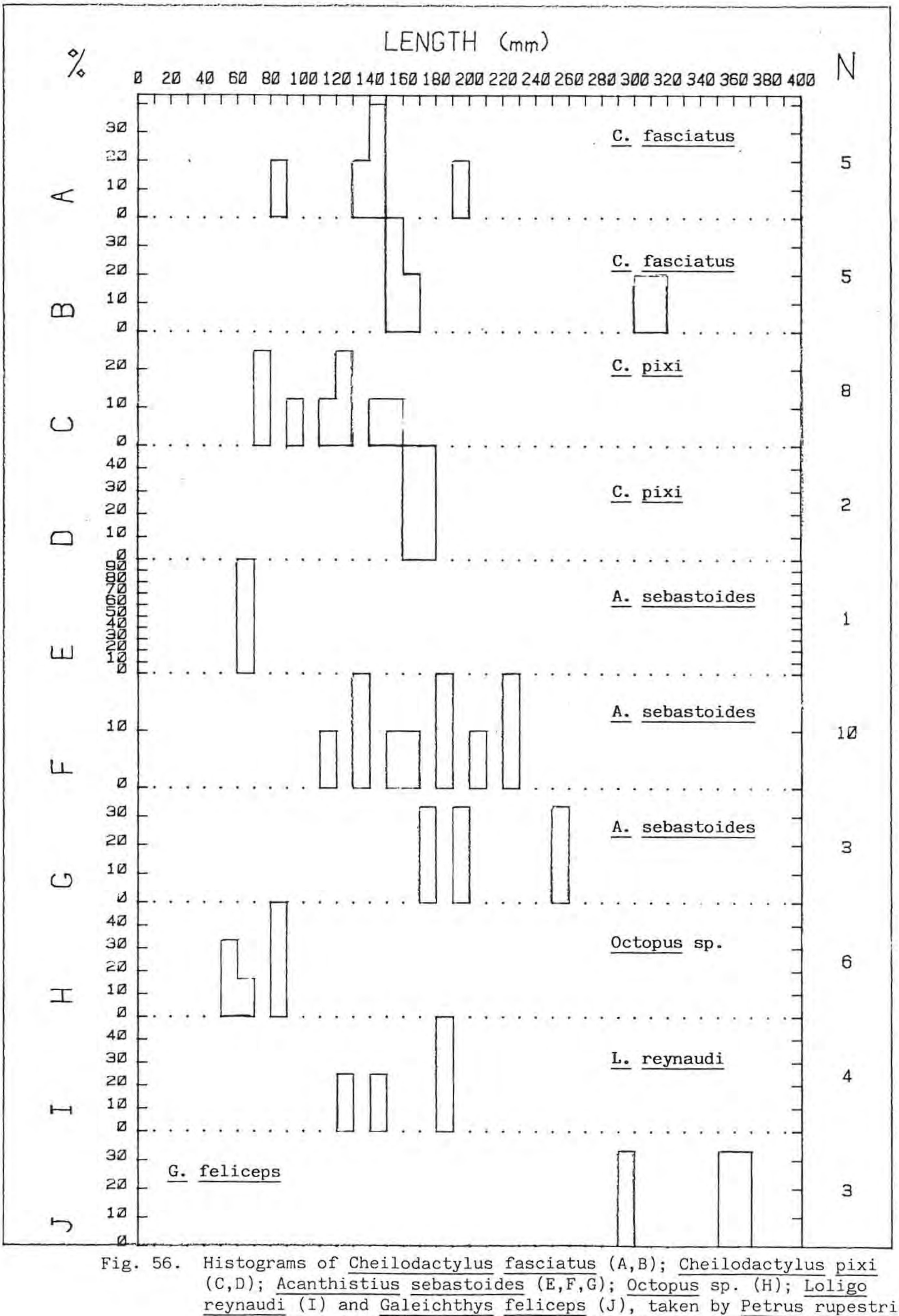


Fig. 56. Histograms of Cheilodactylus fasciatus (A,B); Cheilodactylus pixi (C,D); Acanthistius sebastoides (E,F,G); Octopus sp. (H); Loligo reynaudi (I) and Galeichthys feliceps (J), taken by Petrus rupestris of 200-400mm (A,C,E); 401-700mm (B,D,F) ; 701-1000mm (G) and all size groups (H,I,J).

The lengths of more common prey are shown in histograms in Fig. 56 for the different size groups of P. rupestris. From Figs 55 and 56 it is clear that although there is prey size overlap there is a trend for larger predators to take larger prey.

Behaviour

Observations of predatory behaviour were made in the Tsitsikamma Coastal Park to obtain a clearer understanding of hunting activity. As fishing or spearfishing is banned within this area (except for limited official collections, and shore-based angling along 2 km of the coast) there is a rich fish fauna and many P. rupestris, making it an ideal study site. Behavioural observations were limited as they were only supplementary to other research in the park.

P. rupestris is either solitary or occurs in loosely grouped packs of 2 - 4 fish when larger than 200 mm. Below this size they are rarely seen. A single fish of 55 mm was collected at a rotenone station, suggesting that they are solitary even at this size. Individuals swimming alone have been seen up to about 1000 mm FL. On reefs where several individuals occur over a wide size range, they appear to act independently, swimming in different directions over the reef. Occasionally two or three of approximately the same size swim in the same direction, giving the impression of an opportunistic 'pack' formation. The 'pack' may remain loosely associated for several minutes (often disappearing out of sight after this) or break up, the members diverging and taking different routes over the reef. They 'cruise' over the reef, close to gullies, drop-offs and caves, between one and three metres above the reef. While cruising, the dorsal and anal fin spines are depressed and the pelvic fins are held close to the body (Fig. 57). The rayed section of the dorsal and anal fins projects posteriorly and the pectoral fin is extended, presumably to generate lift. The wide and well-developed caudal fin is moved in a continual series of lateral beats through the broad caudal peduncle. The depth of the body probably offsets the yaw generated. A dark spot on the caudal peduncle is evident until a size approximately 800 mm FL. Periodically they will swim up sheer reef faces of 8 to 10 m. When near the drop-off large fish (>500 mm) are often more abundant in the deeper areas (20 - 25 m).

Fig. 57. Petrus rupestris of about 500mm cruising over a reef. Boopsoidea inornata, Rhabdosargus holubi and Diplodus sargus may be seen in the background.

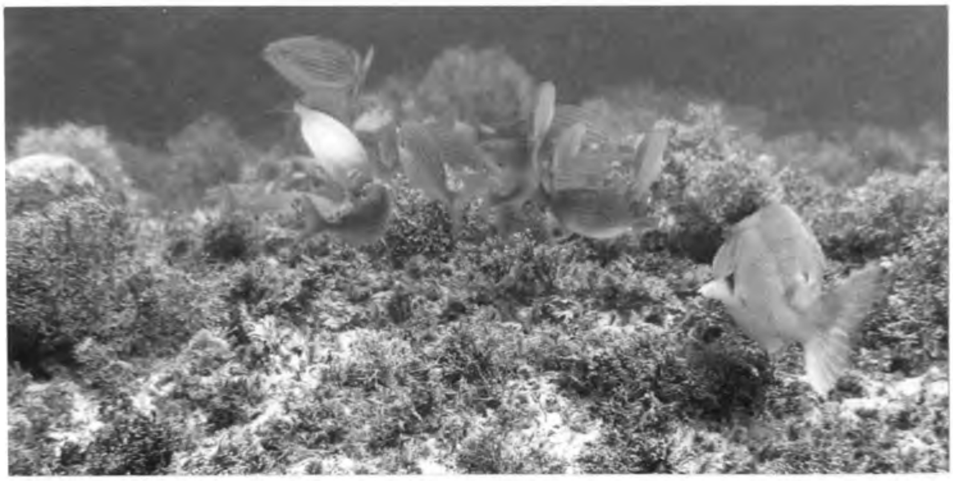


Fig. 58. Petrus rupestris of about 500mm attacking a school of Sarpa salpa.

Fig. 59. Acanthistius sebastoides of 184mm recovered from a Petrus rupestris of 480mm. The teeth marks show that it had been attacked from behind across the ventral surface.

The author has never observed successful pack hunting but the phenomenon is suggested by catches of 5 - 10 P. rupestris of the same size at one reef with the same prey in their stomachs (Genypterus capensis and small catshark), suggesting that they will attack abundant schooling prey.

Individual hunting was observed on several occasions. P. rupestris exhibits two modes of attack, depending on the prey.

1. Solitary prey. The behaviour was similar to that of C. nufar. The quartering speculative dive sequence was as follows: swimming speed increases and the predator swoops down to the reef, often darting into a cave or rushing around an obscuring rock. The aim of these manoeuvres appears to be to take a suitable prey by surprise and to initiate an attack before the prey is aware of the proximity of the predator. When in the open prey seem to freeze or move away when P. rupestris is roughly five body lengths away.
2. Schooling prey. This has been seen most frequently on Sarpa salpa, a herbivore which crops algae throughout the day in schools of 20 to several hundred (pers.obs.). The members of the school feed simultaneously with their head down and the body between 10° and 90° to the surface of the reef. Cropping is an active process. One or two individuals change from the feeding position, bringing their heads into a horizontal position over the rock, then turn and swim off to another patch. The other members join them and vigorous feeding resumes. This active grazing causes the fish to shimmer and reflect light on the shallow reefs. They may attract passing P. rupestris, which often comes in low on the reef, making a rush at the school (Fig.58). The school either opens up (if large) or darts away to another patch to resume grazing when the threat has passed. The attack pattern may be repeated several times by P. rupestris. As was found in C. nufar, some of the approaches, which appear to be undermotivated, may serve to scare off the school to reveal any weak or slow individuals.

Although most commonly found on rugged reefs where gullies, boulders, caves and drop-offs are common, individual P. rupestris may be found on relatively flat reefs which possess few of these features, but they are far less common in such areas and may be passing through.

Examination of prey in stomach contents revealed that fish were invariably in the head-first position, although tooth marks on prey (Fig. 59) reveal they are attacked from behind. This suggests that they are rotated to the head-first position before being swallowed. To observe this in the wild the following experiment was set up: a Pachymetapon aeneum of about 110 mm was shot with a Hawaiian sling armed with a multiprong spear. It was removed and a single hook passed through the body beneath the dorsal fin so that it swam in a normal position. It was still alive and swimming although bleeding slightly. It was lowered from 10 m to 15 m by the SCUBA diver, using a monofilament line. A P. rupestris of 558 mm FL observed it, swam up to it from behind and bit it. The prey was chewed several times (presumably to kill it) with the powerful canines, then rotated in the mouth. At one stage it had part of the fish pinned against a reef while rotating it. The hand-line was kept slack throughout and did not appear to affect any of the behavioural sequence. The fish was swallowed head first and the predator was hooked. The prey was regurgitated while the fish was being subdued. Line fishermen have frequently reported that whole fish bait is chewed by P. rupestris.

Discussion

Petrus rupestris is a large demersal carnivore associated with reefs. It has a robust body and relatively thick caudal peduncle which powers the wide, forked tail. The positioning of the rayed section of the dorsal and anal fins suggests they may serve for breaking, stability and to aid forward motion, as occurs in many teleosts (Gosline 1971). The latter is probably extremely important in rapid acceleration when hunting.

Observations of hunting behaviour during daylight hours, suggest that it hunts by sight and that prey are either solitary or schooling demersal species. Different behaviour patterns were seen for each, and although grouped hunting by P. rupestris was not observed, circumstantial evidence was presented for this. Observations suggest that P. rupestris used its powerful jaws and teeth to attack and masticate prey, including the heavily spined T. feliceps. It seems likely that the catfish is killed and the spines either forced down or broken prior to ingestion. This dentition probably also explains the fairly close correlation of prey size to predator size. Evidently P. rupestris normally hunts relatively large prey. The selection of large prey by big specimens may be related to the gill raker structure, which probably changes ontogenetically. No other studies of hunting behaviour have been made although Penrith (1972) mentions that P. rupestris dart into crevices for food. This is probably the same as the 'speculative dive' behaviour recorded here.

No other detailed studies of feeding have been made although Nepgen (1982) recorded four fish with stomach contents from False Bay. These contained no pelagic fish but S. emarginatum and Clinus sp. were found. Other prey he records are mantis shrimp, amphipods and Turbo sarmaticus and the remains of a brittlestar in one stomach. Regrettably no details of predator size were given. The invertebrates recorded do not accord with observations made in this study.

Stander & Nepgen (1968) observed that P. rupestris occurs over rocky banks and that Octopus, clinids, small roman (Chrysoblephus laticeps) and other reef fish are taken. Again no size is documented but these records agree with this study although C. laticeps was not recorded here.

Intraspecific resource segregation appears to occur by a change of prey species with size. This may result from habitat preferences, larger fish occurring in deeper water than small specimens. The prey size chosen changes with growth and large fish take bigger prey than small predators, although there is some overlap.

Family: Sparidae Polysteganus praeorbitalis (Günther, 1859)
Common name: Scotsman

Description

The body is elongate and laterally compressed. Body depth 36% FL, 46% with the dorsal spines erect (Fig. 3). The lateral line curves smoothly down to the caudal peduncle, running more or less equidistant from the back. The caudal fin is forked, attaching to a fairly robust caudal peduncle. The head is deep, because of the deep preorbital, and its length is about 28% FL; the eye is 4-6% FL. The mouth is moderately large, gape is about 9-12% FL. The 20 - 25 long slender gillrakers occur on the outer gill arch. Dentition comprises four widely spaced canines in the upper jaw and six in the lower. The lateral teeth are conical and fairly stout. An inner band of fine teeth occurs in each jaw. P. praeorbitalis is reddish dorsally. Laterally it becomes paler with the scale edges tinged red. The pink-red head has blue marks around the orbit and blue streaks between the eye and the orbit. This species attains 10 kg at about 90 cm FL but in the eastern Cape smaller fish are more common.

Distribution

P. praeorbitalis is found from southern Mocambique (van der Elst 1981) to Algoa Bay (Smith 1938). As Algoa Bay represents the southern most extreme of its distribution, it is not surprising that those found here are usually small and occur sporadically.

Habitat

P. praeorbitalis is often found in shallow water over reefs, such as near Bird Island and Cape Recife, down to about 20 m. This is considerably shallower than in Natal where van der Elst (1981) records it from 20 - 100 m. The difference in depth distribution is probably related to temperature preferences, and accounts for it being more common in summer and early autumn in the eastern Cape (this study).

Material

A total of 74 P. praeorbitalis between 202 and 668 mm FL were examined between February 1978 and December 1981 (Fig. 60). Thirty-five (202 - 632

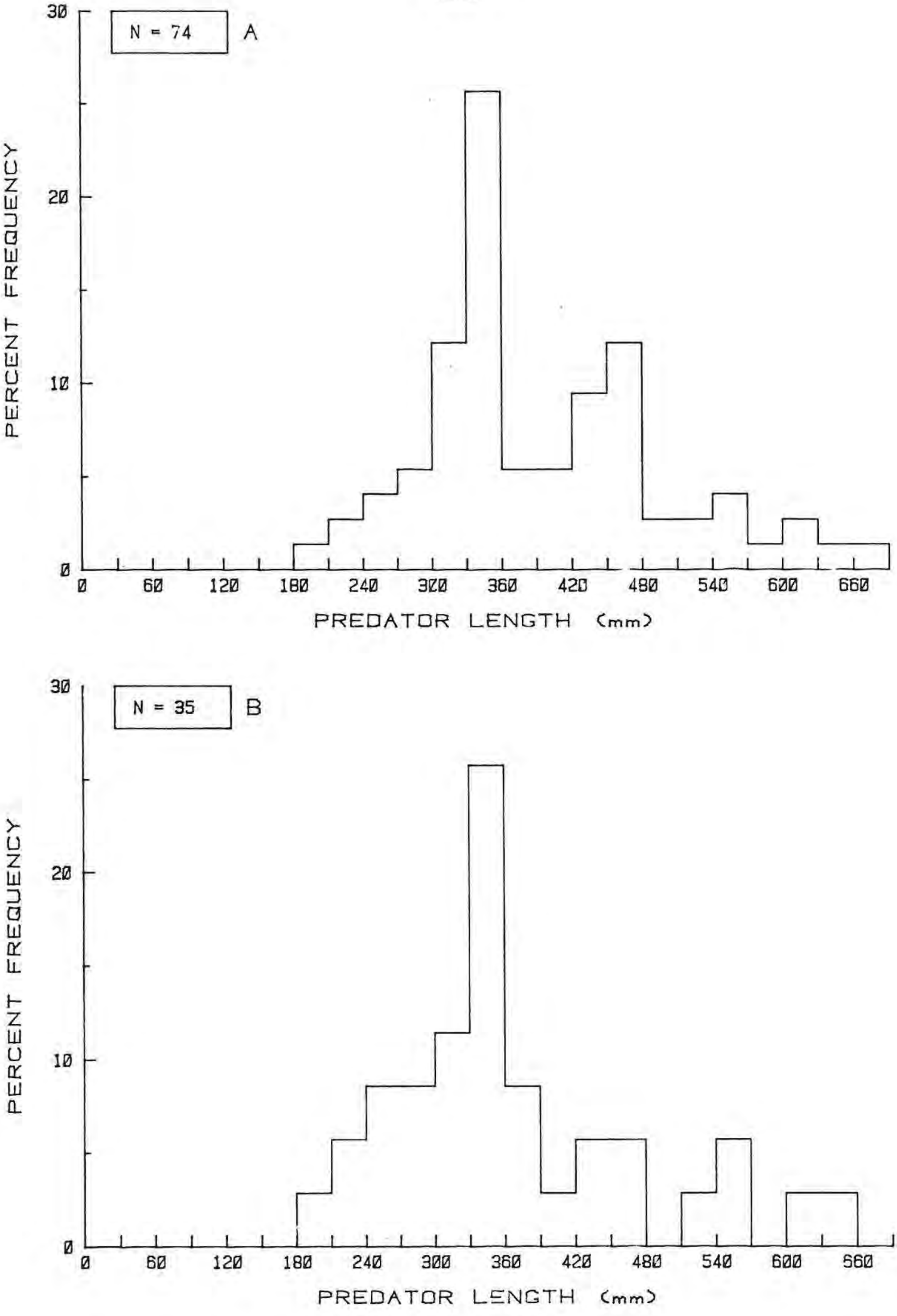


Fig. 60. Histogram of the total sample of <u>Polysteganus</u> <u>praeorbitalis</u> (A) and those with stomach contents (B).

mm FL) had prey remains in their stomachs (47.3%). Of these, 31 were caught by line and four were shot. The highest feeding index recorded was 3.1%. The highest reconstituted stomach mass was 22% of predator mass, which resulted from a large Sepia sp. beak being found in the stomach.

Feeding

The prey of P. praeorbitalis is listed in Table 28 and presented in Fig.61 for three size groups. The 200-300 mm group took copepods and penaeids which accounted for 17% of the number and 3% of the mass of prey. A sepiid was the only cephalopod encountered and it made up 3% and 11% of the number and mass of prey respectively. Fish were the main diet (79%N, 86%M) and all of these were reef-associated or ubiquitous . Clinidae and Cremnochorites capensis were the principal components (41%N, 52%M), although small sparid fishes were also taken. In the 301 - 400 mm group a polychaete, an unidentified crab and Plagusia chabrus made up the invertebrate component of the diet, excluding cephalopods (9%N, 5%M). Sepiidae and octopods were taken by this group (6%N, 20%M) and the balance of the prey consisted of fish, the major prey group (85%N, 75%M). They were all reef-associated or ubiquitous demersal fish except for T. trachurus, a pelagic carangid (4%N, 4%M). Clinidae and Cremnochorites capensis were again the dominant prey (23%N, 28%M) although Gobiidae were also an important group (9%N, 6%M). The Cheilodactylidae, A. sebastoides and sparid fishes made up the balance of the fish prey. The 401 - 700 mm group took fewer crustaceans (Brachyura 5%N, 1%M), but also octopods and L. reynaudi (16%N, 7.M). Bony fishes were the principal prey (79%N, 92%M). The only pelagic fish taken was S. ocellata (11%N, 26%M). Ammodytes capensis, normally associated with sandy substrates, was also taken (11%N, 6%M). The other fish were reef-associated, such as C. brachydactylus, B. inornata, P. aeneum, S. salpa, and Clinidae, including Pavoclinus sp. These made up 53% of the number and 58% of the mass taken.

These results clearly shows that P. praeorbitalis hunts over reefs although a minor proportion of the prey may be taken from the pelagic component, probably as they swim close to reefs. They may be taken in pelagic predators' feeding frenzies. Crustaceans became less important in larger fish and teleosts were principal prey over the size range examined. The dominance of small groups such as the Clinidae and

Table 28. The prey of *Polysteganus praeorbitalis*, according to size.
The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

Prey	200 - 300 mm			301 - 400 mm			401 - 700 mm			Total		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
POLYCHAETA				6.3	2.1	0.4				2.9	1.1	0.1
CRUSTACEA												
Copepoda	11.1	3.4	0.3							2.9	1.1	<0.1
Penaeidea	22.2	13.8	2.3							5.7	4.2	0.1
Brachyura				6.3	2.1	0.7	10.0	5.3	0.5	5.7	2.1	0.5
Plagusia chabrus				12.5	4.3	3.7				5.7	2.1	0.6
MOLLUSCA												
Sepiidae	11.1	3.4	11.1	12.5	4.3	18.1				8.6	3.2	3.1
Loligo reynaudi							10.0	5.3	2.6	2.9	1.1	2.1
Octopoda (Benthic)				6.3	2.1	1.7	10.0	5.3	3.0	5.7	2.1	2.7
Octopus vulgaris							10.0	5.3	1.7	2.9	1.1	1.4
OSTEICHTHYES												
Unidentified fish	22.2	6.9	3.1	25.0	10.6	4.2	10.0	5.3	2.6	20.0	8.4	2.8
Sardinops ocellata							10.0	10.5	25.7	2.9	2.1	20.9
Ammodytes capensis							10.0	10.5	5.7	2.9	2.1	4.6
Cheilodactylidae	22.2	6.9	4.9							5.7	2.1	0.2
Cheilodactylus fasciatus				6.3	2.1	4.1				2.9	1.1	0.6
Cheilodactylus pixi				25.0	12.8	9.0				11.4	6.3	1.4
Chirodactylus brachydactylus				6.3	2.1	2.1	10.0	5.3	1.5	5.7	2.1	1.6
Acanthistius sebastoides				6.3	2.1	12.0				2.9	1.1	1.8
Trachurus trachurus				6.3	4.2	4.1				2.9	2.1	0.6
Sparidae	11.1	3.4	1.2	18.8	6.4	4.6				11.4	4.2	0.7
Boopsoidea inornata							20.0	15.8	35.5	5.7	3.2	28.9
Pachymetopon aeneum							10.0	5.3	7.5	2.9	1.1	6.1
Sarpa salpa	11.1	3.4	12.3				10.0	5.3	10.0	5.7	2.1	8.6
Spondyliosoma emarginatum	11.1	10.3	6.1	12.5	12.8	2.1				8.6	9.5	0.5
Gobiidae	11.1	3.4	6.1	12.5	8.5	5.5				8.6	5.3	1.0
Clinidae	44.4	27.6	24.0	43.8	14.9	20.1	10.0	15.8	2.8	34.3	18.9	6.2
Clinus berrisfordi	11.1	3.4	3.1							2.9	1.1	0.1
Pavoclinus spp.							10.0	5.3	0.9	2.9	1.1	0.7
Cremnochorites capensis	33.3	10.3	24.5	25.0	8.5	7.6				20.0	7.4	2.0
Chorisochismus dentex	11.1	3.4	1.0							2.9	1.1	<0.1
Totals	9	29	16.3	16	47	72.4	10	19	388.8	35	95	477.5

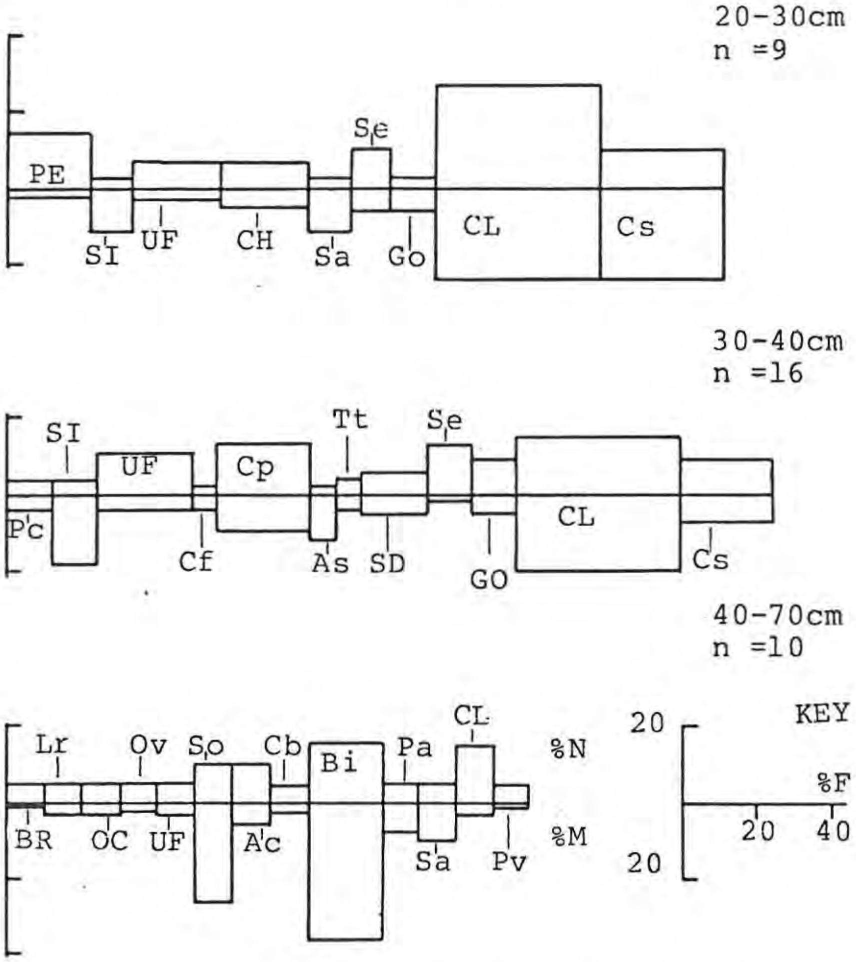


Fig. 61. Principal prey of *Polysteganus praeorbitalis*.

Ac:*Ammodytes capensis* As:*Acanthistius sebastoides* Bi:*Boopsoidea inornata*
BR:Brachyura Cb:*Chirodactylus brachydactylus* Cf:*Cheilodactylus fasciatus*
CH:Cheilodactylidae CL:Clinidae Cp:*Cheilodactylus pixi* Cs:*Cremnochorites capensis*
EU:Euphausiacea GO:Gobiidae Lr:*Loligo reynaudi* OC:Octopoda (Benthic)
Ov:*Octopus vulgaris* Pa:*Pachymetopon aeneum* Pc:*Plagusia chabrus* Pv:*Pavoclinus* spp.
Sa:*Sarpa salpa* SD:Sparidae Se:*Spondyliosoma emarginatum* SI:Sepiidae
So:*Sardinops ocellata* Tt:*Trachurus trachurus* UF:Unidentified fish.

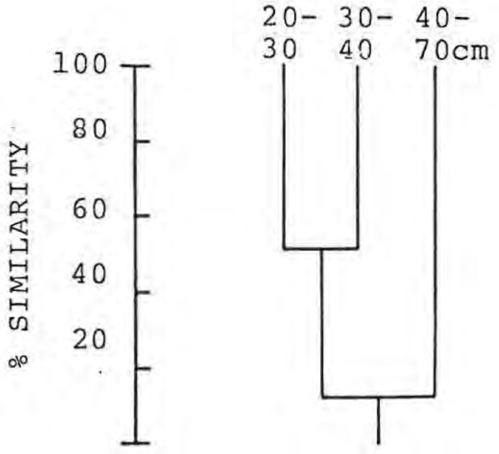


Fig. 62. Similarity dendrogram of diets of *Polysteganus praeorbitalis* size groups, according to prey mass.

Tripterygiidae is reduced and larger fish, such as Sparidae, are taken to a greater extent. The Cheilodactylidae are most important as prey for the Scotsman between 301 and 400 mm. A similarity diagram of diet according to prey mass is shown in Fig. 62. The smaller two groups are most similar (51%) while the large fish are 12% similar to these two.

Predator-prey length relationship

The relationship between *P. praeorbitalis* and its prey is presented in Fig. 63. The minimum and maximum prey is 8% and 49% of the predator length. A feature of the prey is a concomitant increase in size of prey taken with growth and an avoidance of small prey as larger size is attained. Clinids varied between 11% and 38% of predator length: *Cremnochorites capensis* varied between 14 and 21%; *Cheilodactylus pixi* between 14 and 28%; *Spondyliosoma emarginatum* between 8 to 15% of the predator length; *Sarpa salpa* 31% of predator size; octopods varied between 8 and 10% while *L. reynaudi* was 49% of predator length.

Behaviour

Groups or "packs" of *P. praeorbitalis* were observed on three occasions during this study in the shallows at Cape Recife in depths of 4 - 9 m. About five fish measuring about 300 mm FL were swimming more-or-less abreast. Although in loose formation, about 300 to 500 mm apart, they appeared to be aware of each others' movement as they maintained this formation for most of the observation period. Occasionally individuals separated, examining objects among the scattered reefs. On one occasion three of the five were observed with alternating pale and dark horizontal bands along the body, but the cause of this pattern was unclear. Furthermore, it was not obvious why other individuals had the more uniform colouration. As they were sexually immature, it is unlikely to have been sex-related. The swimming formation of the pack was probably effective for covering a wide area. If a small fish had darted to the left or right of a particular individual, those swimming nearby would have been in a suitable position to attack it. On encountering a school of suitable prey the pack could close up and attack in unison, thereby overcoming some of the advantage of prey schooling.

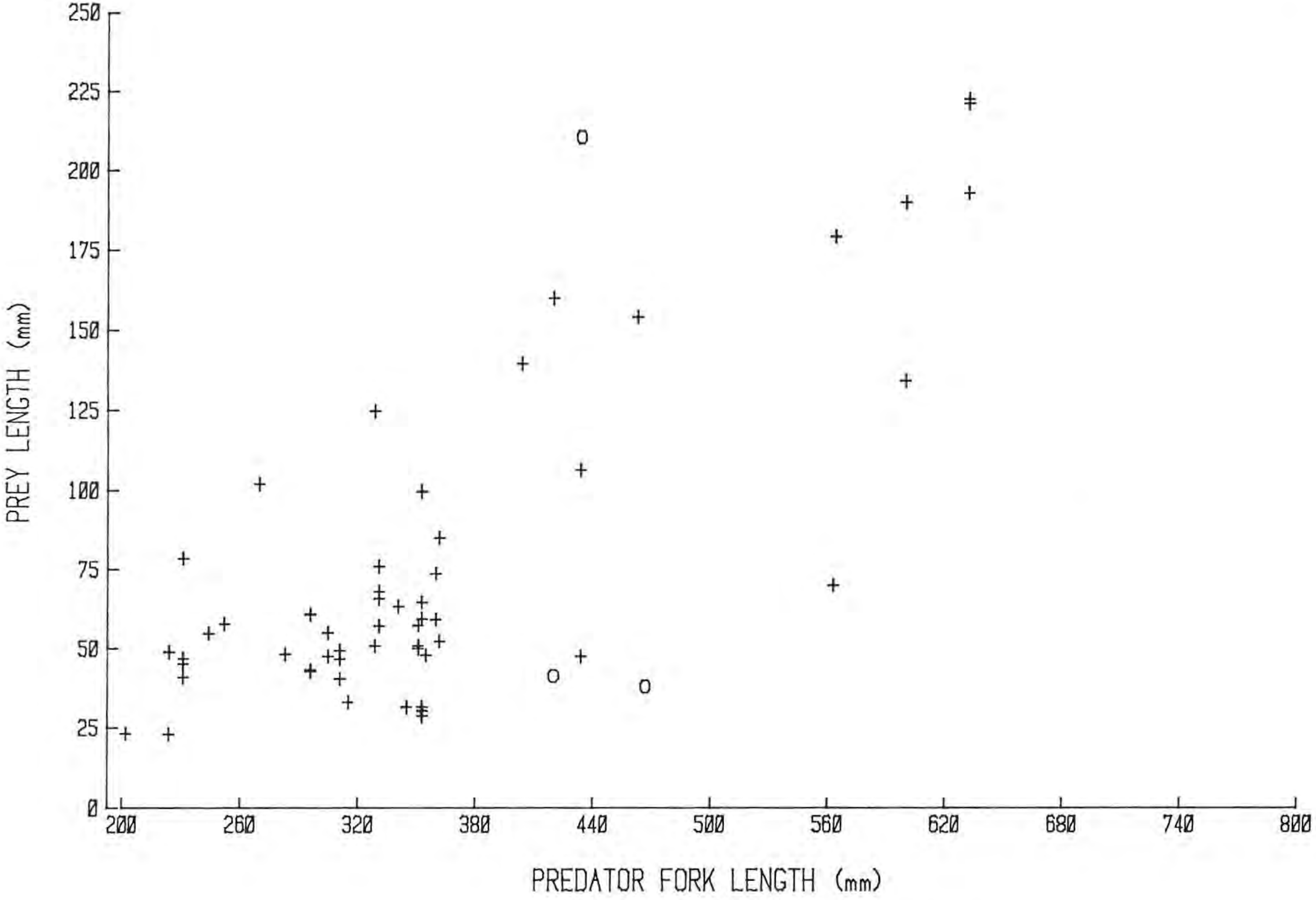


Fig. 63. Scatter diagrams of prey length against fork length of Polysteganus praeorbitalis. Cephalopods are shown by circles and fishes by crosses.

Discussion

Polysteganus praeorbitalis is uncommon in the eastern Cape and is usually encountered in the shallows. No other study on the feeding of P. praeorbitalis has been published although van der Elst (1981) notes that it takes large crabs, crayfish, a variety of reef fish and squid. These observations made from Natal agree with the results of this study although crayfish, which are rare in the shallows of the eastern Cape, were not found during this investigation.

Family: Serranidae Epinephelus guaza (Linnaeus, 1758)
Common name: yellowbelly rockcod

Description

The robust body is slightly compressed laterally (Fig. 3). Body depth is 28 - 32% TL with spines depressed and 38% TL with spines erected. The pectoral fin is paddle-shaped. A simple lateral line curves down to the caudal peduncle. Caudal fin is truncate to rounded, attaching to a robust caudal peduncle. Head is very large, 30% TL. The eye is 5.7% - 3.7% TL and situated close to the dorsal surface. The mouth is large and terminal. The gape is very large, about 16% of TL. The maxillae are strong and long, ending at or just beyond the eye. Strong gill rakers total 20 - 25 and pointed teeth occur in several rows.The body is dark grey-green to brown dorsally and has a yellow ventral surface. Pale blotches on the back and dorsal fins may occasionally give the appearance of having stripes. The species may attain 150 cm; the South African angling record is 25.5 kg (van der Elst 1981).

Distribution

This species is found in the Mediterranean, the north-west coast of Africa, north-east coast of South America, principally on the Brazilian coast, South West Africa and on the west, south and east coasts of South Africa (van der Elst 1981).

Habitat

E. guaza may be found on scattered reefs, massive reef and around artificial structures, such as shipwrecks. They usually lie close to, or on the bottom, either in or near caves into which they retreat and hide. Occasionally they swim about a meter above the reef. They are solitary or occur in pairs in waters as deep as 200 m, although in the eastern Cape they are rarely caught below 50 m. Juveniles have been recorded in intertidal to subtidal rock pools in the eastern Cape (Beckley pers.comm.).

Material

During this study 319 fish between 250 and 875 mm were collected from anglers and spearfishermen, or were shot (Fig. 64). Of these, 90 (301 to 700 mm TL) had prey remains in their stomachs. Fifty-seven of these were collected by line and 33 by speargun. As the prey were similar irrespective of collection method the data were combined. The highest stomach content mass was 10.3% of predator mass. The highest consumption index was 47%, probably caused by octopus beak retention in the stomach.

Feeding

The prey of E. guaza is given in Table 29 and the principal species are shown in Fig. 65, according to three arbitrary size groupings. The 300 - 400 mm group took penaeids, crabs and Plagusia chabrus. The crustaceans made up 70% by number and 58% by mass. Octopus vulgaris was also important, making up 9% of the number and 24% of the mass of prey. The fish component was made up of reef species exclusively, C. fasciatus and C. pixi making up 12% and 9% of the number and mass taken respectively. A total of nine species or groups of fish and invertebrates were found in the 26 stomachs collected. The 401 - 500 mm group also took crustaceans. Panaeids, unidentified crabs and P. chabrus make up 50% by number and 36% of the mass of prey of this group. Unidentified octopods and O. vulgaris made up 15% by number and 34% of the mass. A wider spectrum of fish (9 taxa) was taken by this group, but those identified were all reef-associated or ubiquitous. They represented 35% of the number and 31% of the mass of prey. C. pixi was the principal fish prey (14%F, 11%N, 11%M) and A. sebastoides was secondary (6%F, 4%N, 2%M).

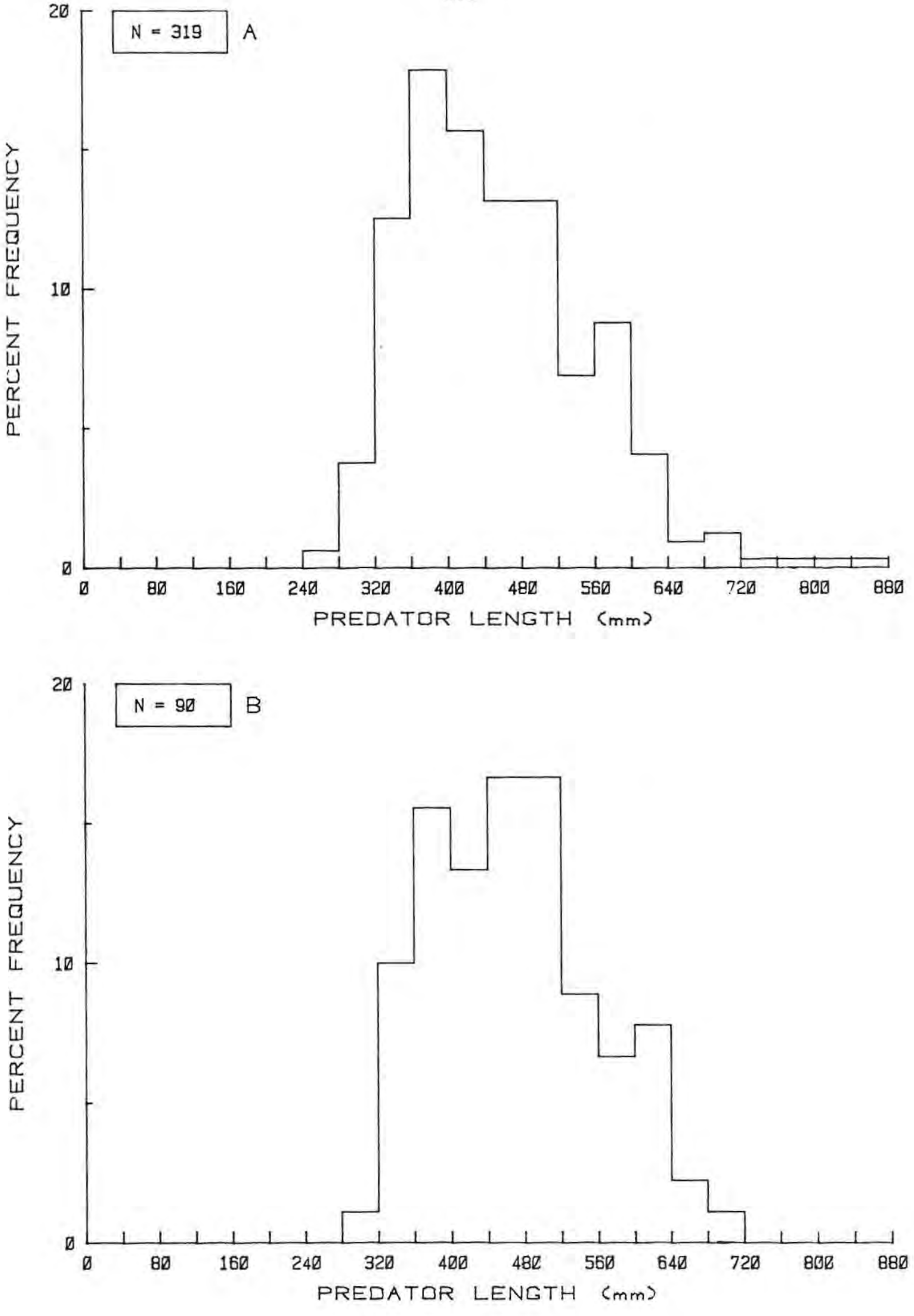


Fig. 64. Histogram of the total sample of Epinephelus guaza (A) and those with stomach contents (B).

Table 29. The prey of *Epinephelus guaza* according to size.
The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g.

	300 - 400 mm			401 - 500 mm			501 - 700 mm			Total		
Prey	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
CRUSTACEA												
Caridea							3.4	43.1	2.1	1.1	20.5	1.4
Penaeidea	15.4	12.1	1.4	2.9	2.2	0.2				5.6	3.3	0.2
Brachyura	34.6	27.3	7.9	37.1	28.3	14.1	10.3	4.2	0.5	27.8	16.6	4.8
Megalopa larvae	3.8	3.0	0.1							1.1	0.7	0.1
Plagusia chabrus	26.9	27.3	49.0	20.0	19.6	21.3	24.1	11.1	11.9	23.3	17.2	17.6
Pseudodromia sp.							3.4	1.4	0.7	1.1	0.7	0.4
Macrura							3.4	1.4	5.1	1.1	0.7	3.3
MOLLUSCA												
Sepiidae							3.4	1.4	0.2	1.1	0.7	0.1
Loligo reynaudi							6.9	2.8	6.1	2.2	1.3	4.0
Octopoda (Benthic)				2.9	2.2	0.1	10.3	4.2	0.5	4.4	2.6	0.3
Octopus vulgaris	11.5	9.1	24.1	17.1	13.0	33.8	20.7	11.1	50.3	16.7	11.3	43.7
CHONDRICHTHYES							3.4	1.4	0.2	1.1	0.7	0.2
OSTEICHTHYES												
Unidentified fish	7.7	6.1	7.6	8.6	6.5	3.3	3.4	1.4	1.7	6.7	4.0	2.6
Bothidae							3.4	1.4	7.1	1.1	0.7	4.6
Cynoglossus capensis							3.4	1.4	1.9	1.1	0.7	1.2
Cheilodactylidae				2.9	2.2	0.1				1.1	0.7	<0.1
Cheilodcatylus fasciatus	7.7	6.1	5.3	2.9	2.2	2.2				3.3	2.0	1.0
Cheilodcatylus pixi	7.7	6.1	3.9	14.3	10.9	11.1	3.4	1.4	0.3	8.9	5.3	3.5
Chirodactylus brachydactylus				2.9	2.2	2.8	3.4	1.4	0.6	2.2	1.3	1.1
Acanthistius sebastoides				5.7	4.3	2.1				2.2	1.3	0.6
Boopsoidea inornata							3.4	1.4	2.6	1.1	0.7	1.7
Diplodus cervinus				2.9	2.2	1.8				1.1	0.7	0.5
Lithognathus mormyrus							3.4	1.4	<0.1	1.1	0.7	<0.1
Pachymetopon aeneum							3.4	1.4	0.2	1.1	0.7	0.1
Spondyliosoma emarginatum							3.4	1.4	0.2	1.1	0.7	0.2
Clinidae	3.8	3.0	0.7	2.9	2.2	4.7	3.4	1.4	0.1	3.3	2.0	1.4
Congridae							3.4	1.4	3.3	1.1	0.7	2.2
Conger wilsoni				2.9	2.2	2.4	6.9	2.8	4.4	3.3	2.0	3.5
Totals	26	33	216.3	35	46	674	29	72	1644	90	151	2534.3

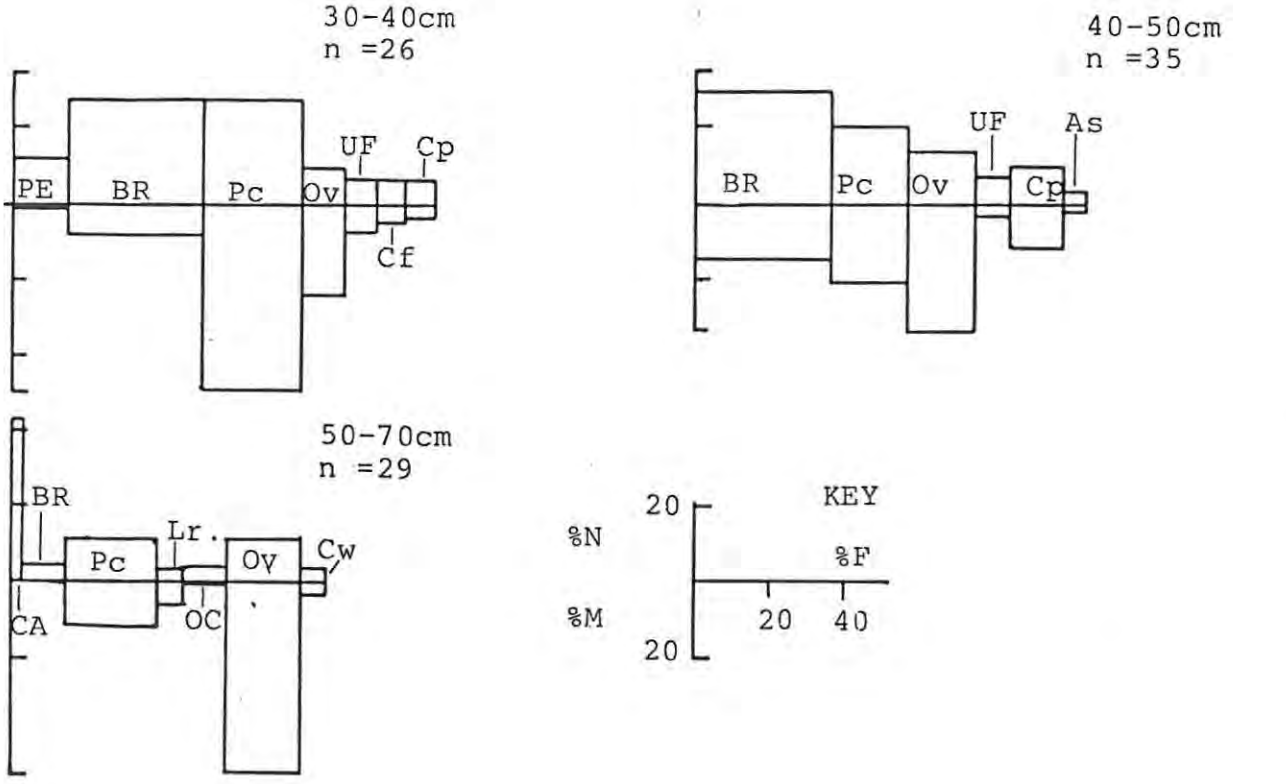


Fig. 65. Principal prey of Epinephelus guaza.

As:Acanthistius sebastoides BR:Brachyura CA:Caridea Cf:Cheilodactylus fasciatus Cp:Cheilodactylus pixi Cw:Conger wilsoni Lr:Loligo reynaudi OC:Octopoda (Benthic) Ov:Octopus vulgaris Pc:Plagusia chabrus UF:Unidentified fish

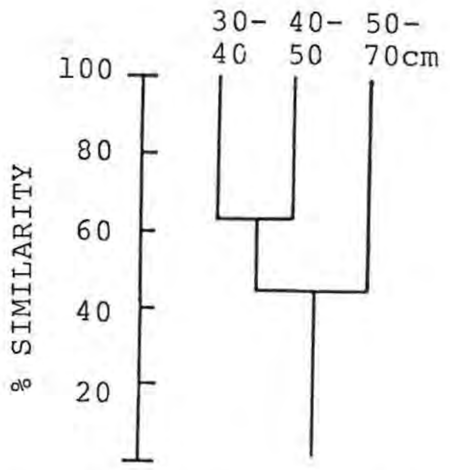


Fig. 66. Similarity dendrogram of diets of Epinephelus guaza size groups, according to prey mass.

Crustaceans were major prey of the 501 - 700 mm group, representing 61% of the number and 20% by mass of the prey taken. Caridae were represented by a large number (31) of *Plesionika* from the stomach of a fish from East London. *P. chabrus* was important by frequency (24%), number (11%) and mass (12%). Cephalopods were represented by sepiids, *L. reynaudi* and octopods. *O.vulgaris* was the most important prey in this group (21%F, 11%N and 50%M) and the most dominant of all prey groups by mass. Thirteen groups of fish were identified. Three were soft substrate-associated: Bothidae, *C. capensis* and *L. mormyrus*, although the latter is often found adjacent to reefs on sand. This group made up 4% of the number and 9% of the mass of prey. The wide range of species taken in low numbers caused them to become insignificant individually, consequently none except *C. wilsoni* are shown in Fig. 65. The reef fish identified were *C. pixi*, *C. brachydactylus*, *B. inornata*, *P. aeneum*, *S. emarginatum* and Clinidae, they constituted 8% by number and 4% by mass of the diet. Conger eels made up 4% of the number and 8% of prey mass.

Over the size range examined, crabs and octopods were therefore the principal species taken. Two species of particular importance were *P. chabrus* and *O. vulgaris*. Reef fish made up the majority of the teleost prey, indicating that *E. guaza* preys principally on species closely associated with reef systems. The large array of prey other than the two species mentioned above suggests opportunism. The importance of the two invertebrates may suggest the abundance of these prey, but could also imply that the rockcod is in fact a specialist, which will take other prey when the preferred prey are absent. A similarity dendrogram (Fig. 66) is shown for the size groups discussed.

Predator-prey length relationship

A scatter diagram of prey length against *E. guaza* total length is presented in Fig.67. The relationship between prey and predator length varied between 4 and 108% of the predator length. The smallest prey taken were crustaceans, such as *Plagusia chabrus* (5 - 10% of predator length) and carideans, while the largest were congrid eels, which have very elongate bodies. Apart from the congrid eels, most fish taken were between 15 and 56% of the predator length. Octopods varied between 9 and 32% of the total length (mantle length of octopods being measured). The congrid eels varied between 77 and 108% of the total length and were

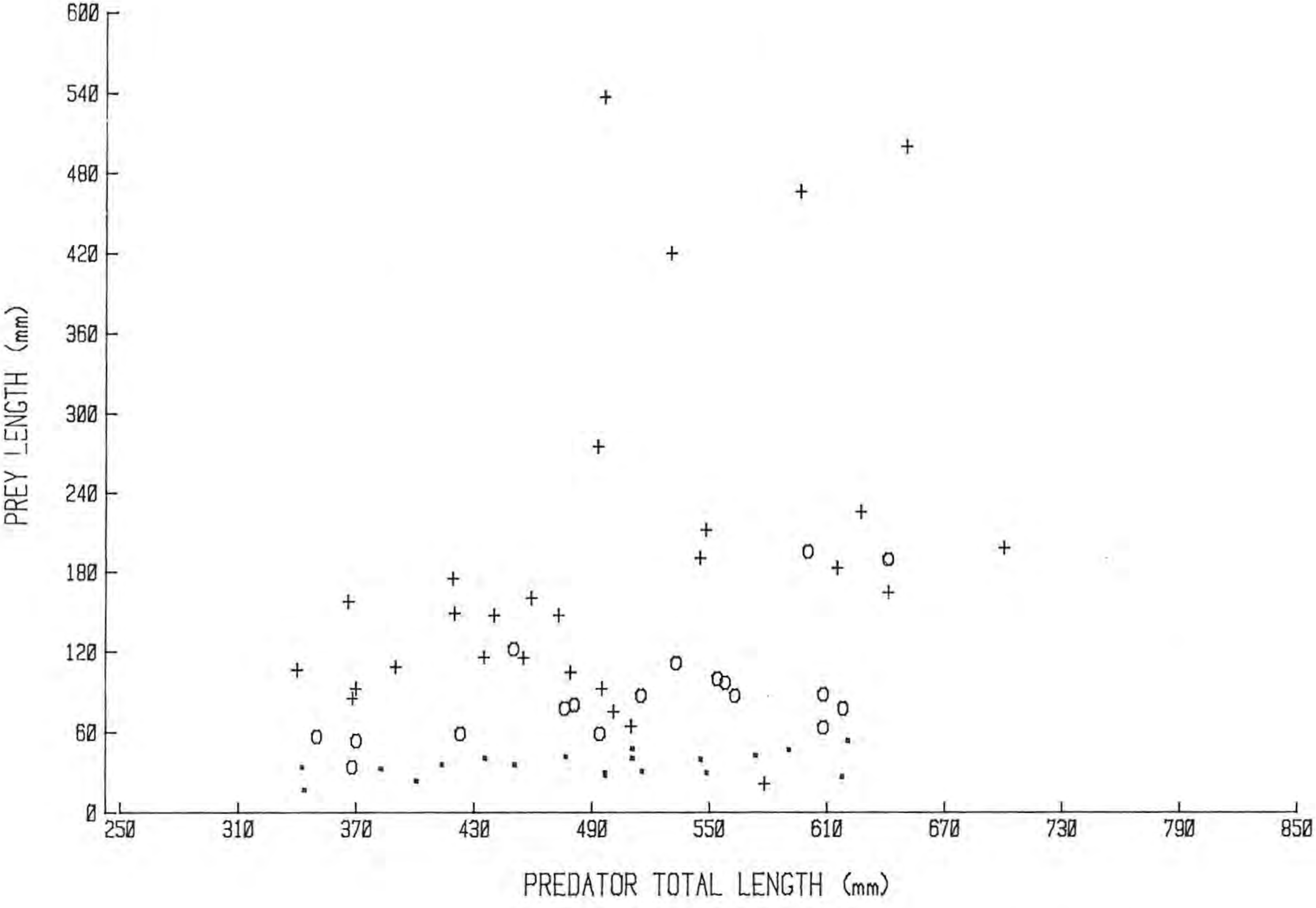


Fig. 67. Scatter diagram of prey against total length of *Epinephelus guaza*. Crustaceans are shown by dots, cephalopods by circles and fishes by crosses.

folded in the stomach. Apart from the eels, the prey size taken over the range shows considerable overlap.

Discussion

Epinephelus guaza is a benthic reef-associated species usually found near caves. With its cryptic colouration the fish is easily overlooked as it rests on the bottom, stabilizing itself with its paddle-like pectoral fins. Like their congeners, they are ambush predators (Randall 1967, Hobson 1968, Collette & Talbot 1972, Harmelin-Vivien & Bouchon 1976). They lie in wait for a prey to approach closely, then charge and engulf the victim with the large mouth and by expanding the opercula. The rows of small teeth are ideal for grasping octopods.

E. guaza is evidently a diurnal predator as prey were often found undigested in the stomachs of fish collected by day. No information on crepuscular or nocturnal behaviour was collected in this study. Collette & Talbot (1972) record that E. guttatus, E. adscensionis, E. striatus, E. cruentatus, E. fulvus, Mycteroperca venenosa and M. tigris are common diurnal and crepuscular predators in the Virgin Islands. Stark & Davis (1966) found that rock cods fed by day and night, with a peak at sunset in the Florida Keys. Hobson (1968) found that Epinephelus labrifrons feeds throughout the day and night, but perhaps more productively at night. On the other hand, he found that Mycteroperca roseacea is principally crepuscular and feeds on schooling flatiron herring, Harengula thrissina, when the predator is larger than 300 mm. Harmelin-Vivien & Bouchon (1976) found the Serranidae from Tulear, Madagascar, feed throughout the day but more actively at night. From these accounts, it appears that feeding times vary between species, perhaps depending on the activity of the preferred prey.

It is worth noting that crabs and octopods are important prey over the entire size range. Crabs are often more active by night (pers.obs.). Octopods vacate their caves at night to hunt for food (Altman, 1967, Kayes 1974, Nigmatullin & Ostapenko 1976) although they also forage short distances from their lairs during the day and small specimens may be seen abroad by day (Smale & Buchan 1981 and this study). At such times they are particularly vulnerable to predation, although it is not clear whether rockcods are able to attack them successfully in their lairs.

However, freshly ingested specimens of both groups were found during the day, when E. guaza is seen to be active on reefs. It is therefore likely that the yellowbelly rockcod is diurnal and may be crepuscular in feeding habits.

The majority of the fish taken are reef-associated, indicating that most of the feeding is done over reefs. However, a few of the fish taken such as Bothidae and Cynoglossidae are associated with sandy substrates. They are probably taken by those individuals inhabiting the edges of reefs, although these are minor prey species. Lithognathus lithognathus is also usually found over sand flats during the day but at night it approaches reefs where it would be vulnerable to predation by E. guaza.

The prey of E. guaza changed with increasing predator size. Crustaceans became less important with growth, while octopods and fish became more dominant. Similar findings are reported on Epinephelus striatus in the West Indies. Randall (1967) reports that the larger fish feed more on fish and less on crustaceans than did the smaller specimens and noted that small rockcods are often diurnal. Harmelin-Vivien & Bouchon (1976) similarly found that prey of small Epinephelus merra (60- 90 mm) took brachyurans predominantly and relatively fewer fish . The larger group (100 - 240 mm) took few brachyurans but a large quantity of fish, and cephalopods.

In addition to a change in importance of prey groups, it was found that the food of the larger group is more varied than small fish and that the maximum prey size increases with growth. The size of the prey of large E. guaza overlapped with that of the small rockcod.

E guaza is not abundant in the eastern Cape, although to what extent this results from angling exploitation is unclear, as these large carnivores are known to be the first to be fished out of the reef habitat (Randall 1982).

Reef fish discussion

A distinguishing feature of reef fish predator-prey interactions and those of pelagic and open sand environments is the heterogenous reef surface which is covered by encrusting organisms. The relief is determined largely by the geological structure. Wave action and sand scouring influence the biotic components and spatial complexity of the microhabitats. Diving observations during this study have revealed that the number and size of fishes and the number of species is generally greater where there is high relief. This is consistent with other studies (Stark & Davis 1966). Over the flat reefs, particularly if there is sand scour, the diversity of invertebrates and fishes seems to be lower.

It has been shown in Natal that on shallow subtidal reefs, which are highly influenced by both heavy wave action and cyclical erosion and deposition of sand, mobile fauna such as rock lobsters and octopus move off the reef when subject to high sanding levels (Smale 1978, Buchan & Smale 1981). On the other hand sessile invertebrates may die off periodically (Jackson 1976, Berry 1978, 1982). Such physical stress is not apparently characteristic of massive reefs which have been examined repeatedly in this study. This is particularly so with deep reefs which have a rich fauna and flora and are tens of meters higher than the sand levels. In these cases the trophic complexity is well developed with Pyura, octocorals and sponges being dominant. Reef fish are commonly seen in such areas using the cover afforded.

The advantage of cover to prey in avoiding predation is well known and has been described for various habitats by several authors. Jackson (1961) hypothesises that riverine spawning migrations upstream and subsequent choice of vegetated habitats for young fish are largely induced by predation pressure (especially by Hydrocyon vittatus and Lates niloticus) in African freshwater systems. He also suggested that these predators have retarded speciation in their prey. In the ensuing controversy Fryer (1965) and Greenwood (1965) argued against some of Jackson's ideas, although Greenwood expands on the importance of cover in the early life history of Tilapia, Protopterus and Clarias. Kok (1980) also reported that potential prey species of H. vittatus abound among the numerous aquatic macrophytes in the shallows of the Pongolo floodplain. This probably results from antipredator behaviour. Keast (1978) has also noted that aquatic macrophytes of Lake Opinicon afford protection to small prey fish, although protection is not complete as young perch and pike pursue prey even there. However, he believes that experiments will be necessary to determine the effects predators have on faunal distribution. Keast & Harker (1977) have previously demonstrated that other factors, such as food distribution, may largely be responsible for fish distribution.

In estuaries Whitfield & Blaber (1978) have shown that predation by piscivorous teleosts is lower on those species inhabiting littoral vegetated areas. Blaber (1982) has described feeding of the barracudas, *Sphyraena jello* and *Sphyraena barracuda*, whose juveniles exploit vegetated areas, preying on larvae sheltering there, although large fish and adults move into open water.

Several studies of marine fishes have highlighted the benefit of structurally complex habitats like reefs as refuges against predation. These include classic studies such as Hiatt & Strasburg (1960) on the coral reefs of the Marshall Islands, and Hobson's (1968) study in the Gulf of California. Hobson (1968) describes the result of more than 1200 hours of observations of fish interactions and notes the importance of schooling, diurnal-nocturnal activity patterns and the susceptibility of fishes to predation depending on the time of day. Stark & Davis (1966) describe the habits of fishes and the use of shelters by several species. They also describe the use of shelter by individual grunts once they are detached from schools when pursued by carangids. Similarly, Hartline *et al.* (1972) describe how a school of plankton-feeding *Chromis cyaneus* flees to the shelter of a coral head when approached by predators such as carangids, lutjanids and sphyraenids. This escape response ensured that the *Chromis* were safely in the coral head before the predators were close enough to attack. Interestingly, they succeeded only partially against trumpet fish which succeeded in attacks, apparently by hovering motionless before the rush. Similarly, lizardfish also made successful attacks as the *Chromis* appeared not to have a suitable escape mechanism against this predator. Potts (1980) describes the reactions of prey to attacks by *Caranx* and shows how schools of lutjanids, mullids and *Gerres* use the advantages of schooling with the spatial complexity of reefs to escape. His descriptions agree well with behaviour seen during this study in reactions between *Sarpa salpa* and other young sparids when subjected to predation by *Cheimerius nufar* and *P. rupestris*. Similarly, other prey species such as Monodactylus falciformis, Gymnocrotaphus curvidens and Diplodus sargus appear to use reef structures in their escape behaviour. Thus there appears to be general agreement on the strategic benefit of reefs and other protective structures.

These observations have been confirmed in laboratory studies and in modelling. Ware (1972) examined the feeding behaviour of rainbow trout (Salmo gairdneri) presented with different prey sizes and density on substrates of varying complexity. He found that the intensity of predation and total food consumption was inversely related to the complexity of the substrate because a number of prey were able to escape detection by finding cover. Similarly Stein (1977) showed that crayfish suffer less predation with increased substrate particle size as they have effective refuges. Glass (1971) found that increased structural diversity of aquaria resulted in reduced capture rate of prey (guppies Lebistes reticularis) and fewer attempts at predation by largemouth bass (Micropterus salmoides). However at low complexitiy the prey could be decimated.

Many small reef fishes are seen individually and are characterised by cryptic colouration. They are often immobile for long periods (Hobson 1968, 1974, Feder et al. 1974, Helfman 1978). In this study Clinidae, Gobiidae, Cheilodactylidae, Batrachoididae and the serranid Acanthistius sebastoides were examples of this group. They are often associated with small patches of algae or found in depressions in the reef. On the reef they are easily overlooked. They obviously benefit from crypsis and immobility not only in reducing predation on them but also (presumably) in intercepting their own prey. Observations on "speculative dives" at the reefs and into caves by the predatory sparids were described previously and evidence that this was to frighten prey into flight and thus make them more vulnerable to attack was discussed. This behaviour appears to be specifically aimed at cryptic individual prey. Another attack pattern described was the use of reefs and boulders to conceal the approach of predators. Similar behaviour has been reviewed by Curio (1976) for both terrestrial and aquatic animals. Epinephelus guaza, on the other hand, appears to be an ambush predator which lies immobile until prey are close enough to be attacked.

Top reef predators examined in this study were all diurnal although peaks of activity were not detected, largely because of inadequate diving time and samples were collected by day from fishermen. The importance of octopus and crabs in the diet of *Epinephelus guaza* may infer that the species is more crepuscular or nocturnal as these prey are usually more active and exposed at night when foraging (Kayes, 1974, Ebeling & Bray 1976, Nigmatullin & Ostapenko 1976, Smale & Buchan 1981). However, prey were often found to be undigested when the predators were collected during the day, which infers diurnal activity, as do observations of rockcod lurking about during the day. Similar plasticity was reported by Harmelin-Vivien & Bouchon (1976) in a study of serranids and scorpaenids in Madagascar.

Several common features were found in the predation of reef carnivores. Firstly, there is an ontogenetic change of diet, crustaceans becoming less important with an increase in size. Ontogenetic changes in diet with large carnivorous fishes have been shown by numerous authors including Hobson (1968) for cabrilla (*Mycteroperca roseacea*), Harmelin-Vivien & Bouchon (1976) for *Epinephelus merra*, and several other examples in the present study. Most of the reef predator's diet is comprised of reef prey although soft bottom demersal species are also taken, probably when close to reefs and vulnerable to these predators. *Cheimerius nufar* larger than 400 mm, largely take pelagic fish although much of this sample was collected when pilchards, *S. ocellata*, were abundant in Algoa Bay and thus may be biased towards the pelagic component. However, it is clear that pelagic species are taken to a far greater extent by *C. nufar* than by other reef fishes. *A. argyrozona* appears to be an even more pelagic sparid (Chapter 4), while *C. nufar* appears to be plastic in its feeding, taking both demersal and pelagic fishes. Cephalopods are important prey of all the reef predators discussed here and particularly *E. guaza*.

Although very little is known about the biology, ecology or feeding of the prey species encountered in this study, it seems that the majority of reef prey eat small crustacea and other invertebrates. This holds for octopods (Smale & Buchan 1981), *Cheilodactylus fasciatus* and *Chirodactylus brachydactylus* (Butler 1975) and some Gobiidae (Butler 1980). Christensen (1978) reported that *Diplodus sargus*, *D. cervinus* and *Sarpa salpa* juveniles feed largely on small crustaceans although *S. salpa* becomes herbivorous when adult. These findings were confirmed by Joubert & Hanekom (1980) working on large fishes in Natal. Finally, Stobbs (1980) records that the gobiesocid *Chorisochismus dentex* feeds largely on small crustaceans and juveniles but also takes sea urchins and limpets. Examination of the stomach contents of *Acanthistius sebastoides* revealed that this species feeds largely on small crabs and to a lesser extent small fishes. Thus the top carnivorous teleost examined during this study feed on first to third level carnivores. The food web of top predatory reef fishes is, therefore, very largely reef-based.

In each top predator, Cheilodactylidae and octopods were found to be important prey. The length frequency of each prey group for the four predators is shown in Fig. 68, where all sizes of predator are combined. It appears that on size criteria alone *C. nufar* and *P. praeorbitalis* overlap most in selection of cheilodactylids and octopods. Similarly the prey size of *E. guaza* and *P. rupestris* shows most overlap, although it should be remembered that size selection depends on predator size. Thus small specimens of *E. guaza* and *P. rupestris* will select prey in a similar size range as *C. nufar* and *P. praeorbitalis*. This overlap cannot be considered to be competition (*sensu* Sale 1979) as there is no evidence of limited availability of prey. It should be noted that all the reef fish are relatively rarely seen and caught although *C. nufar* is the most abundant of the species. This is suggested by the total number of predators examined in this study. These totalled 3235 for *C. nufar*, 751 for *P. rupestris*, 74 for *P. praeorbitalis* and 319 for *E. guaza*. Although the figures cannot be used for accurate population size estimates, they clearly show the relative abundance of the predators, which are also borne out by underwater observations. Although these figures result from several factors, two possible reasons should be considered.

The relatively low numbers of reef predators may be a reflection of reproductive strategy, the low numbers of *P. rupestris* and *E. guaza* exhibiting 'k' selection (Odum 1971, MacArthur 1972) which infers that they have evolved towards maintaining equilibrium densities and may also have low growth rates. This may be a result of their specialised reef

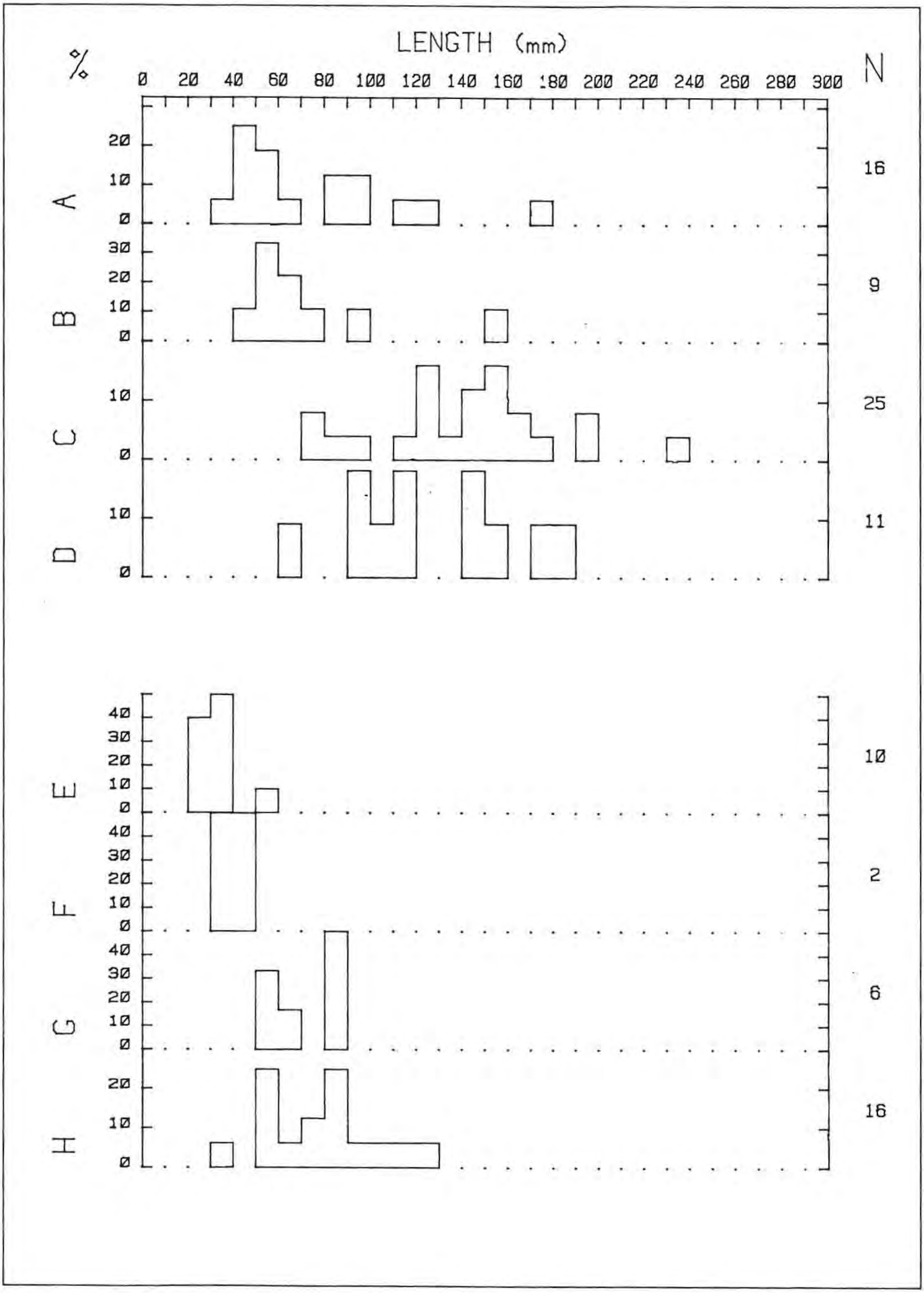


Fig. 68. Histograms of prey common to the reef predators. Cheilodactylidae (A,B,C,D) and Octopus sp. (E,F,G,H) taken by all sizes of Cheimerius nufar (A.E), Polysteganus praeorbitalis (B,F) Petrus rupestris (C,G) and Epinephelus guaza (D,H).

predator function as they are carnivores of the upper trophic levels. C. nufar, however, may be exhibiting more of an "r" strategy, possibly with a faster growth rate, reducing competition both inter- and intra-specifically by its feeding plasticity, apparently being more of an opportunist. Reduction in potential competition between these species may be further increased by habitat differentiation. Although nothing is known about the residence patterns of these fish, large serranids are generally believed to inhabit reefs for long periods (Hobson 1968, Randall 1982). Differential habitat selection has frequently been documented as a strategy which may reduce potential competition in fishes (Keast et al. 1978, Helfman 1978, Sale 1979). The mechanisms involved in habitat selection are obscure. Sale (1975) has suggested that similar species of small pomacentrids on the Great Barrier Reef use the same kinds of territories. In their case the priority of arrival of recruits rather than subtle differences in habitat requirements or competitive abilities of adults may determine which species hold the sites. This system probably does not hold with warm temperate top predatory species which breed and recruit over a shorter time period. Behavioural interactions may be more important as some of the species appear to be semi-resident, but this needs further investigation.

A factor which has had considerable impact on reef fishes is line fishing. Randall (1982) notes that the larger carnivorous fishes are the first to be fished out of a reef habitat whatever the fishing method. This group includes the species discussed here, especially as they are prime eating and sport fish. This impact is even greater when the species are slow growing, exhibit sexual reversal and are resident. Expanding on this idea, Regeier et al. (1979) suggested that fishing out large old fishes, characteristic of "virgin" and perhaps stable communities able to withstand environmental fluctuations, causes scramble competiton in a community. Regrettably there are no catch records available in the eastern Cape to confirm that exploitation of large carnivorous fishes has had an effect on the population, although this seems extremely likely, as Biden (1930) recorded that species such as P. rupestris were commonly observed at the beginning of the century, while this no longer applies, apart from in the Tsitsikamma Coastal National Park. The impact of exploiting these fishes will be discussed in more detail below.

CHAPTER 7

A SIMILARITY ANALYSIS OF TOP PREDATORY TELEOSTS IN EASTERN CAPE COASTAL WATERS.

In previous chapters the prey of each predator has been discussed in relation to size, locality and time. The inter-relationships between species are less clear. In order to investigate this each species size group is analysed below to determine their similarity. Data were separated according to locality for tunas.

Methods

The similarity analyses were run according to the method of Field et al. (1982) who argue the merits of the analyical strategy they use, which supercedes that of previous studies (e.g. Field 1969, 1970, Field & McFarland 1968). The comparisons were made on original wet weight values which were normalised to percentage for each predator size group. No root-root transformation was used, as the mass of diets is thought to give a good representation of diet with generally large samples.

The measurement of similarity used was the Bray-Curtis measure which has the form:

$$\delta_{jk} = \frac{\sum_{i=1}^{s} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{s} (Y_{ij} + Y_{ik})}$$

Where Yij = score for the ith species in the jth sample;

Yik = score for the ith species in the kth sample;

δjk = dissimilarity between the jth and kth samples summed over all S species. δjk ranges from 0 (identical scores for all species) to 1 (no species in common) and is the complement of the similarity Sjk:

Sjk = 1 - δjk

The measure is not affected by joint absences and is therefore sufficiently robust for marine surveys or stomach content analyses where more than half the data entries may be zeros. Furthermore, it gives weight to more abundant species in comparing the samples (Field et al. 1982).

Classification was performed by group-average sorting, which joins two groups of samples together at the average level of similarity between all members of one group and all members of the other (Field et al. 1982). The result is diplayed as a dendrogram and the cut-off levels used are arbitrary. As Field et al. (1982) point out, four main disadvantages detract from the simplicity of dendrograms:

1. The identity of a sample is lost once it is placed in a group.
2. The dendrogram shows the inter-group relationships and the level of similarity shown is the average inter-group value.
3. The sequence of the individuals (predator size categories) is arbitrary and two adjacent samples are not necessarily the most similar.
4. Dendrograms may force a graded series into discrete classes by overemphasizing discontinuities.

Finally, it should be noted that there is no accepted method of statistically testing the significance of differences between groups which are linked, as the assumptions of the tests are not met (Field et al. 1982).

These disadvantages may be overcome by using an alternative presentation to illustrate individual relationships, to determine whether discontinuities are real. This may be done by delineating dendrogram classes on the ordination diagram (Field et al. 1982).

Ordination was done by multi-dimensional scaling which produces an ordination of the predators in a specified number of dimensions. The goodness of fit was measured by a stress formula which indicates by large stress that the "map" tallies poorly with the observed dissimilarities. Conversely, with low stress the sample relationships are well represented in the specified number of dimensions. Stress may be thought of as the distortion resulting from "compressing" the data to fewer dimensions. The final "map" is only determined to within an arbitrary orientation and reflection, and arbitrary location and scale. Consequently the axes are omitted in Figs. 70 and 71 (Field et al. 1982).

The following discussion will test the complementary hypotheses that numerical analyses of stomach content data (a) give the same conclusions on feeding groups (pelagic, soft-bottom demersal and reef) as was reasoned in Chapters 4 - 6, and (b) illustrates ontogenetic changes in the diets of the predators.

Results and Discussion

Classification

Fig 69 shows that there is clear grouping at high similarity levels (>60%), especially at the top of the figure. At the bottom, linkages between groups start at lower levels and, at the very bottom, a few of the samples (e.g. 15,19) show very little similarity with any of the other groups and therefore link at extremely low levels of similarity. The broken line at the 10% level of similarity gives two large groups of predators as well as a minor grouping and two outliers (i.e. as yet unlinked). This division segregates those carnivores taking mainly or exclusively pelagic prey (A) and those taking principally or exclusively reef-dwelling prey (B). The outliers, with the exception of A. hololepidotus, are also predatory reef fish.

The above groups will be examined briefly to determine links between component species. It should be noted that in these numerical analyses no data on prey size was included as this would have increased the complexity of the analyses. The similarity described applies to prey species genera or higher taxonomic groups. In many cases similarity would be further reduced if a measure of size were included. Fig. 69 shows the linking predator groups, the higher levels of which will be used as illustrations. Two yellowfin tuna groups (801 - 1400 and 601 - 800 mm) taken at East London form a linkage at the 61% level. Next to this group are three size groups of T. albacares taken inshore, which show very high levels of similarity. Atractoscion aequidens (300 - 600 mm) links at the 71% level. Joining this group at the 62% level is a group made up of inshore caught Katsuwonus pelamis (601 - 700 mm), Cheimerus nufar (400 - 700 mm), inshore caught Katsuwonus pelamis (501 - 600 mm) and large Atractoscion aequidens (601 - 1000 mm) . Lichia amia (701 - 1200 mm), Seriola lalandi (401 - 700 mm), Lichia amia (401 -700 mm) and Polysteganus praeorbitalis (401 - 700 mm) join the group at lower levels.

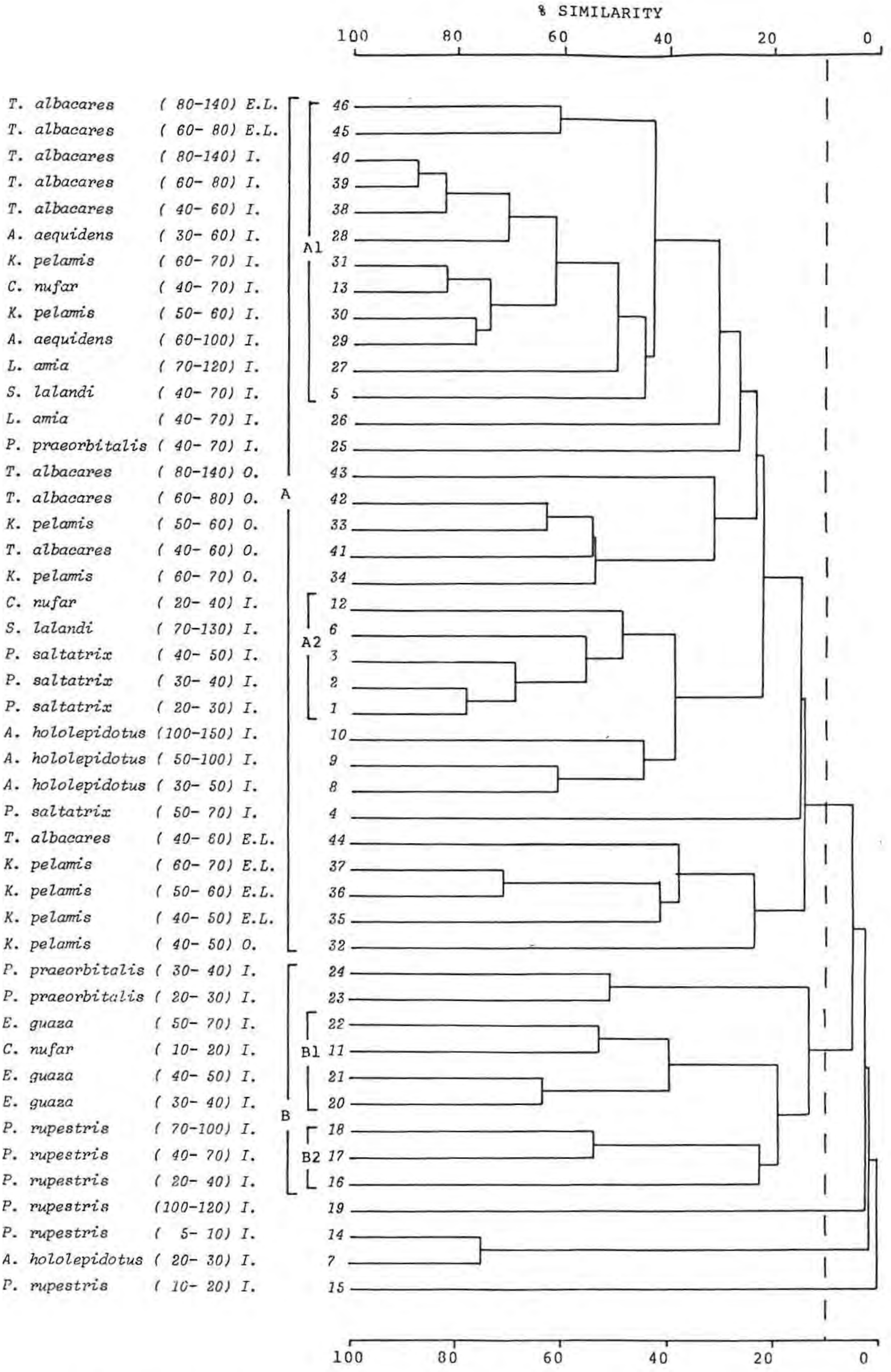


Fig. 69. Dendrogram showing classification of 11 teleost predators which have been segregated by size into 46 groups. The abundance measure of prey mass was used, and comparisons were made using the Bray-Curtis measure. The dendrogram was formed by group average sorting. The groups A and B are explained in the text. Two main groups are formed at an arbitrary similarity level of 10%.

Another group, whose components link between 50 and 70% similarity, comprises offshore caught T. albacares (601 - 800 mm) and K. pelamis (501 - 600 mm), T. albacares (401 - 600 mm), and K. pelamis (601 - 700 mm). The largest group of T. albacares caught in the same area links at 31% similarity to the group.

Another fairly distinct sub-group comprises Pomatomus saltatrix (201 - 300 mm), P. saltatrix (301 - 400 mm), P. saltatrix (401 - 500 mm), Seriola lalandi (701 - 1300 mm) and C. nufar (201 - 400 mm). They share such prey as clupeids, engraulids and Loligo reynaudi, for example. Linking onto this group at 39% is a group of Argyrosomus hololepidotus of 301 - 500 mm, 501 - 1000 mm and >1000 mm, which linked at a higher level of similarity. Large P. saltatrix (>500 mm) only link onto this entire group at 15% similarity, showing little similarity to the rest of the group.

Another sub-group of tuna caught at East London consisted of T. albacares (400 - 600 mm). K.pelamis of 601 - 700 mm, 501 - 600 mm and 401 - 500 mm link to K. pelamis caught offshore at 23% similarity.

Group B predators (Fig. 69) comprise Polysteganus praeorbitalis of 301 - 400 mm and 201 - 300 mm; Epinephelus guaza (>500 mm) and C. nufar (100 - 200 mm). (The latter linkage results largely from Octopus vulgaris being major prey species to both but in reality the size selection of prey is considerably different. The linkage of these two predators clearly illustrates the disadvantage of not taking prey size into consideration). E. guaza of 401 - 500 and 301 - 400 link and this entire sub-group links to Petrus rupestris of 701 - 1000 mm, 401 - 700 mm and 201 - 400 mm at the 19% level. These groups represent the reef predators which share several prey species.

Outliers comprise P. rupestris of >1000 mm and 100 - 200 mm. They are outliers partly on account of their low numbers, giving disproportionate weight to the few prey encountered. Large P. rupestris preyed on fish which were not recorded in the other predators. The similarity of juvenile P. rupestris (50 - 100 mm) and small kob (200 - 300 mm) resulted from mysids being taken by both. These prey were generally too digested for reliable identification. However, the few that were identified suggest that P. rupestris take reef-dwelling species such as Mysidopsis similis while A. hololepidotus take the prolific swarmers such as Mesopedopsis slabberi. This linkage may therefore be considerably higher than is really the case because accurate identification was generally not possible.

Ordination

The two groups A and B, identified by classification and drawn on the dendrogram are illustrated in the ordination diagram. (Fig. 70), following the method of Field et al. (1982). The numbers assigned to the predators are the same in both figures. The stress of the 2-D plot is 0.1822 (Fig. 70). The change from 3-D (0.1306) is low and suggests that the data are adequatly represented in this plot. Stress always increases when the number of dimensions is reduced (Field et al. 1982); at 1-D a stress of 0.3 was observed.

The clustering of predators into two groups and their spatial separation conforms with the dendrogram. Furthermore the "outliers" identified from the dendrogram are distant from the two groups which have been outlined.

For the sake of simplicity only four sub-groups have been illustrated within the major groups. The groups B1 and B2 correlate with the dendrogram. The three size groups of E. guaza and C. nufar (B1) cluster as do three size groups of P. rupestris of B2.

The sub-group A1 conforms well with a sub-grouping of the dendrogram while A2 is less tightly clustered. This may be found with undelineated sub-groups such as that formed by A. hololepidotus and tuna not caught inshore. It probably reflects the complexity of inter-relationships of fish which prey on similar species. Had it been possible to integrate a measure of prey size selection, the predator groups would certainly have separated more. This would have given more information on prey partitioning.

Some idea of the change of inter-relationships between co-occurring predators is given in Fig. 71 where the different size groups of predators are linked. This indicates how the potential competitors change

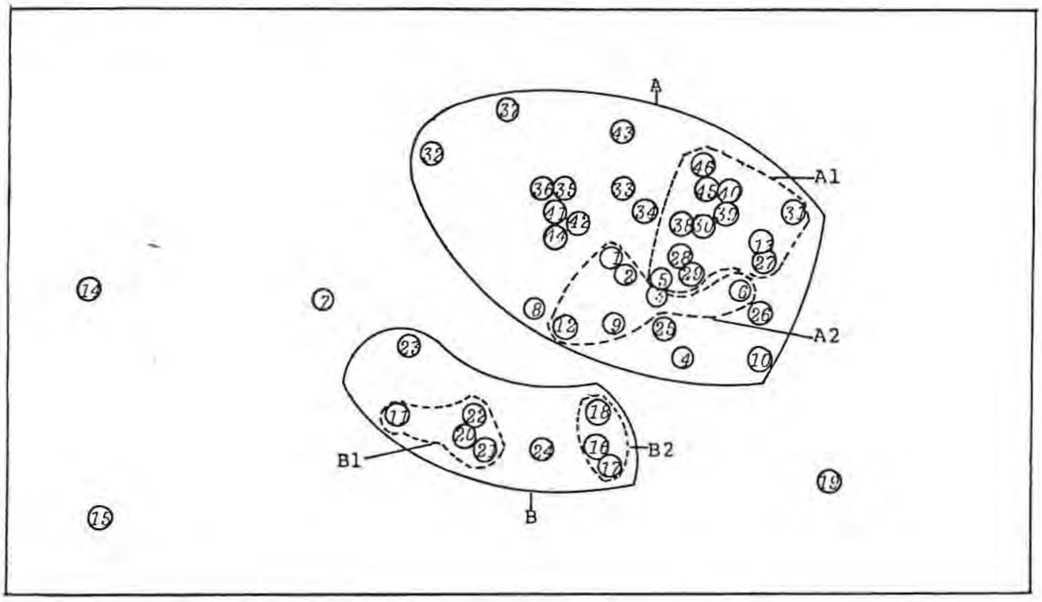


Fig. 70. Ordination of 11 teleost predators which have been segregated by size into 46 groups. The sample numbers conform with Fig. 83 and the groups A and B are explained in the text. The axes scales are arbitrary and therefore not shown.

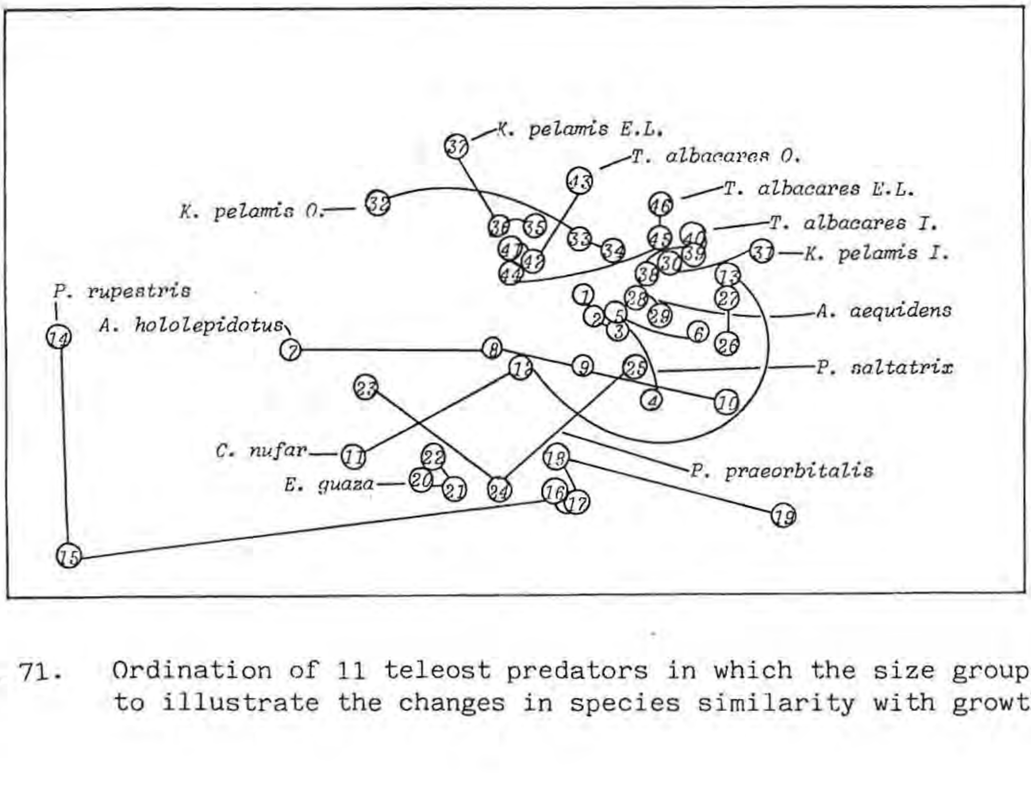


Fig. 71. Ordination of 11 teleost predators in which the size groups are linked to illustrate the changes in species similarity with growth.

ontogenetically, although it should again be mentioned that no account has been taken of changes in prey size with growth.

The tuna species, T. albacares and K. pelamis, exhibit relatively small changes in location with an increase in size, especially those caught inshore, as they take the highly abundant schools of pelagic prey, most notably clupeids and engraulids. Offshore size groups differ more (for example K. pelamis, numbers 32, 33 and 34 and T. albacares 41, 42 and 43) which was shown earlier and is thought to result from greater patchiness and the lower availability of prey in oceanic waters. Furthermore it was shown that tuna venture into inshore waters over a restricted period, particularly January to April, but they mainly inhabit offshore areas.

The relative positions of the inshore pelagic predators change little with growth, for example A. aequidens (28 and 29), L. amia (26 and 27) and S. lalandi (5 and 6). However, bearing in mind that the relative proportions of prey strongly differ between the two size groups, the figure may not describe the changes very well. This was found to result from reducing the data to two dimensions. The similarity in diet of P. saltatrix groups is reflected in their proximity (numbers 1 to 4), while the large group was found earlier to differ most and is here shown to be most separated from the rest.

The soft bottom demersal predator A. hololepidotus shows marked spatial variation in Fig. 71 compared to the other species size groupings. This results from the wide variety of prey taken, varying from mysids to relatively large fish such as other kob and demersal fishes. The marked difference of the largest group may result partially from the relatively low number of specimens available. Its position at the 'lower' end of the pelagic predator group results from sharing common prey species such as L. reynaudi, S. ocellata, engraulids and some demersal species with pelagic predators and illustrates overlap in food resources.

The reef predators show similar changes in relationships. C. nufar, for example, shows marked change and it appears to be highly opportunistic, either taking reef prey or seasonally abundant pelagic prey. This opportunism has probably caused a displacement of the position of the large group (13) as they took mainly pelagic prey. It seems likely that more material over a greater proportion of the year would reveal that more reef fish are taken. This is confirmed by data collected by Garrett (pers.comm.) in Natal.

Polysteganus praeorbitalis (23 - 25) shows marked changes, initially preying on small invertebrates and reef fish, and later taking larger reef fish, finally feeding on passing schools of pelagic prey which it shares with pelagic predators and kob. Epinephelus guaza assemble in a remarkably tight group, which in part reflects the limited size range of predators collected (301 - 700 mm). It suggests that food partitioning is not clear cut because they take the same prey types.

P. rupestris prey varies dramatically with growth over the size range available (55 mm - 1186 mm). Small mysids are important initially but fish such as gobies are taken by 190 mm specimens. The prey species of the next three size groups is similar although the prey size selected varies with predator size. Finally, large reef fish are taken by the largest P. rupestris.

Conclusions

These analyses have shown that the top predatory teleosts may be divided into two broad groups at the 10% level of similarity; those which feed largely on reef fishes and those which take pelagic or soft-bottom demersal species. The sub-groups show varying levels of similarity but these were most similar for schooling pelagic predators which take highly abundant coastal engraulids and clupeids. Although no account was taken of prey size or habitat, overlaps were less than 80% similar for all but 5 groups. The diets of the reef fish groups differed more than diets of the pelagic predators. The ordination diagram revealed that despite the identity of predators being lost by grouping, good agreement was found between the two analysis methods. The ordination diagram was used to illustrate ontogenetic changes in relationship between predators and it revealed the species with which they had most similarity at various sizes. The differences between size groups suggested a more gradual change in diet with growth in the ordination. This agrees well with observed differences and confirms that the dendrogram tends to overemphasize differences (Field et al. 1982) and illustrates the need for both analytical methods. Generally these analyses confirm observations made in previous chapters. The results will be discussed in relation to other resource partitioning studies below.

CHAPTER 8

GENERAL DISCUSSION

The sampling methods used to determine food exploitation in fishes require critical review to facilitate legitimate and meaningful interpretations (Hyatt 1979). This will be the purpose of the following pages, after which the findings made in this study of resource partitioning will be compared to similar work elsewhere and broad research needs will be identified. The use of such studies for resource management will also be discussed.

Methodology review

Almost all of the stomach material of the eleven carnivorous fishes discussed in this study was collected from ski-boat catches. Limited data obtained on prey taken from speared fish or nets, however, conformed well with line-caught fish. It is worth considering why the results obtained from different methods were similar, while other authors recorded that line-caught fish reveal a different prey spectrum to those caught by trawling or longline (e.g. Baxter 1960, Nepgen 1979). The major reason for this similarity is that stomach contents of line- caught fish were sampled effectively only to about 30 m and diving collections, too, did not exceed this depth. The similarity is therefore not unexpected. An attempt to collect from greater depths was made using gillnets, but only monofilament material was available and this was destroyed during trials, presumably by sharks, so the attempt had to be abandoned. Material collected at greater depths and different localities would be different - as was demonstrated with A. hololepidotus in this study. It should be noted, furthermore, that the tuna collected offshore showed different feeding patterns. This was attributed to different prey availability offshore and possibly different feeding depths being exploited by different sized predators.

Feeding indices may be used to provide an estimate of feeding rate in the field (Bruton 1979), but the frequency of regurgitation, which resulted from capture stress, change in depth and gas bladder expansion severely limited the usefullness of mean fullness values in this study. Maxima were given throughout, however. In addition, as the fishes were attempting to feed on the bait or lure at the time of capture, they would probably have had little in their stomachs (Randall 1967), which would bias mean values towards 'hungry' fish. In the case of the tunas, however, the maximum and mean values appeared to be less influenced by these problems, partly because they were caught by surface trolling. The results obtained from T. albacares and K. pelamis, therefore were used to compare with data collected in other studies. It is clear that alternative sampling methods need to be used to overcome problems with regurgitation in studies of diurnal or seasonal changes in feeding rates of deep-living marine fishes. Possibly the use of explosives or intensive spearfishing may overcome these problems. Furthermore, digestion rates should be studied in the laboratory (Magnuson 1969) and compared to field studies. Finally, it should be noted that consumption indices may be influenced by the retention of cephalopod beaks (e.g. S. lalandi, T. albacares, C. nufar). Until estimates of retention time are made, it will be difficult to use consumption indices in quantitative estimates of food intake rates.

The results obtained during this study are not generally representative of the entire populations of predators as the predator species have a greater depth and geographic distribution than the study area. Unfortunately there is no available estimate of the proportion of the populations at the various depths. Neither is there an estimate of their number, or size composition. The ski-boat catch survey has, however, given a preliminary estimate of their relative proportions and the size distribution of large fishes in the eastern Cape. The effects of gear selectivity are unrecorded and population estimates based on one method alone are questionable. The results obtained during this study are, therefore, largely descriptive. They have, however, provided a valuable insight into the interactions of the top predators of major food webs in coastal areas and have given the first detailed account of their prey.

A noteworthy advantage of collecting material from ski-boats was that a wide variety of areas are sampled, providing information on local habitat variation. A disadvantage was that small fishes were under-represented because of gear selectivity (see also Potts 1981).

A question raised by this study and others is: "To what degree are the predators selecting prey?" Although there is an inference that each group of predators takes either pelagic, soft demersal or reef prey respectively (despite some overlap), it was only possible to investigate selectivity in A. hololepidotus. Even this study was preliminary, however, as material collected over several years (from kob) may not be entirely compatible with trawls made over a few days in two months of one year. Further studies are needed which compare collections made by trawling with predators caught by another method, perhaps explosives. Generally the time and financial burden is prohibitive in selectivity studies of marine piscivores. As Keast (1970) has noted, it is difficult to obtain detailed ecological and trophic information from the marine environment. Quast (1968) details the cost of quantitative collections of reef fishes in the sea and the inherent difficulties which need to be overcome to obtain more information on prey selection. This partially accounts for Sale's (1980) observation that the only area of real understanding of reef fish trophic relationships is that between plants and herbivores. This could be partially resolved using study methods such as those of Major (1978) who used large experimental pens in a natural lagoon to investigate behavioural interactions of piscivores and their prey.

Squid beaks and fish otoliths were extremely valuable in reliable identifications and size estimates of prey. Long term storage of these samples will allow them to be re-examined in future, either in age studies of prey or when more reliable identifications of squid are possible by comparing ratios between structural features (Wolff 1982). The difficulties of identifying octopods and some squid families have been noted previously (Clarke 1962, Pinkas et al. 1971, Perin et al. 1973, Imber 1975, 1976, Ross 1979, Clarke 1980, Clarke in prep.) Only continued research and development of other methods of prey identification will resolve these problems. Among the teleost prey, gobies, clinids, triplefins and early juveniles were the most difficult to identify. Hopefully these problems will be overcome once a more representative otolith collection of small reef fish has been built up. Reliable identification of other prey to the species level not only provides information on the predators but allows a better understanding of prey distribution and size composition (see discussion of Chapter 4).

Two problems were encountered in this study which prevented an accurate reconstitution of stomach content weights. The first was that no suitable method was developed to allow for differential digestion of prey such as crustaceans and fish. Secondly there was a notable retention of squid beaks in the stomach contents of predators. These problems have been encountered and discussed by previous authors (e.g. Windell, 1971, Hyatt 1979, Tricas 1979, Clarke 1980, Hyslop 1980). The discrepancies vary between predators and require laboratory examination to make adequate allowance for the reconstruction of stomach contents. Although this was not attempted in this study, it needs to be done before stomach contents can be accurately reconstructed for energetics studies.

The approach used in this thesis was to study all the teleost predators simultaneously. The advantage is that differences observed between them are less likely to be influenced by the availability of prey over the study period. The disadvantage is that such broad coverage is extremely time consuming, which limits other related research. Consequently a good overall pattern of feeding by teleost predators in shallow coastal waters was obtained, but it was not possible to devote much time to other aspects, such as observations of predator-prey interactions or experimental manipulations. Diving work and observations of display animals was undertaken whenever possible, which assisted the interpretation of data collected from stomach content analyses.

As a field study this work has provided good insight into the prey taken by teleosts at the top of the food chain. Experimental manipulations and further studies of interactions underwater are now needed. Further observations such as those made by Hobson (1965, 1968, 1972, 1974) and Potts (1969, 1970, 1980,1981) would provide valuable information. Studies could be augmented by in situ experiments such as those by Hartline _et al_. (1972) and Hurley & Hartline (1974) for a better understanding of behavioural interactions and to clarify the co-evolution of predator and prey.

The eastern Cape coastal food web of teleosts at upper trophic levels.

A summary of the feeding inter-relationships determined in this study is pertinent. The three systems (pelagic, soft demersal and reef) have been synthesized on two diagrams, Fig. 72 and 73. The similarlity analysis of Chapter 7 revealed that *A. hololepidotus* has prey in common with some of the more pelagic species, hence its inclusion there. As this study concentrated on inshore fishes, predation by the two tunas offshore is not included. Furthermore, no allowance has been made for prey size selection, which has already been shown to be an important aspect of resource partitioning. Values over 4% mass are illustrated and the direction of energy flow is indicated.

Key species of the inshore pelagic food web are *Sardinops ocellata, Engraulis capensis* and *Loligo reynaudi* (Fig. 72). Other important pelagic species taken are *Etrumeus teres* (especially juveniles), *Trachurus trachurus* and *Scomber japonicus*. With the exception of *L. reynaudi*, these species are all planktivores. Despite the importance of the above species to carnivorous teleosts, demersal species such as *Pagellus natalensis, Cheimerius nufar* and the Sepiidae are also important to *L. amia* and *A. aequidens*, both of which often hunt in relatively shallow water. *P. saltatrix* feeds both pelagically and demersally, which is evident in Fig. 72. This agrees with the findings of other workers (e.g. Grant 1962, van der Elst 1976, Sykes & Manooch 1979). The proportion of demersal prey increases in older elf. *Argyrosomus hololepidotus* is largely a demersal feeder although it will take highly abundant schooling species. Diet overlap in intermediate size groups 300 - 1000 mm was offset by prey size selection. Cannabalism was noted in both *A. hololepidotus* and in the few *Merluccius capensis* sampled. The reciprocal predation on these two species is noteworthy. This was thought to reduce potential competition between them. The predation patterns of *M. capensis, Thrysitis atun, Argyrozona argyrozona* and *Sarda sarda* are included here as they provide further insight into the importance of the key prey in this area.

The importance of a few abundant and therefore principal prey in food webs has been encountered in studies of both estuaries (e.g. Whitfield & Blaber 1978, Marais pers. comm.) as well as in the sea (Davies 1949, Rand 1960, Nepgen 1979, Randall *et al*. 1981, Batchelor 1982, Furness & Cooper 1982, Nepgen 1982). Similarly, Morejohn *et al*. (1978) found that four major prey items formed the basis of the food web in Monterey Bay. In that area squid, anchovy, rockfish and krill are the principal components of

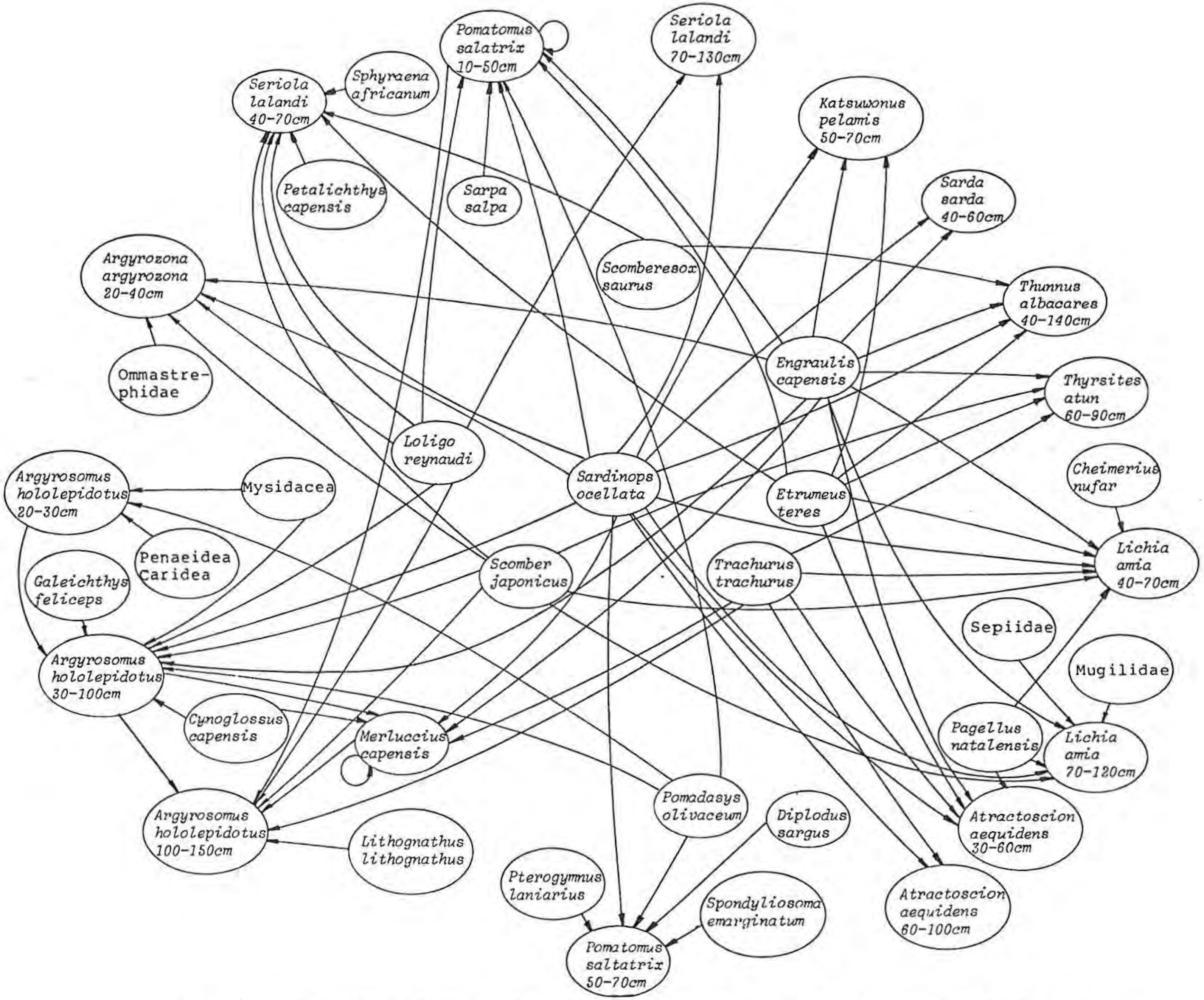


Fig. 72. The pelagic and soft-bottom demersal food web of coastal areas in the eastern Cape. Prey making up more than 4% by mass of the predators stomach contents are shown.

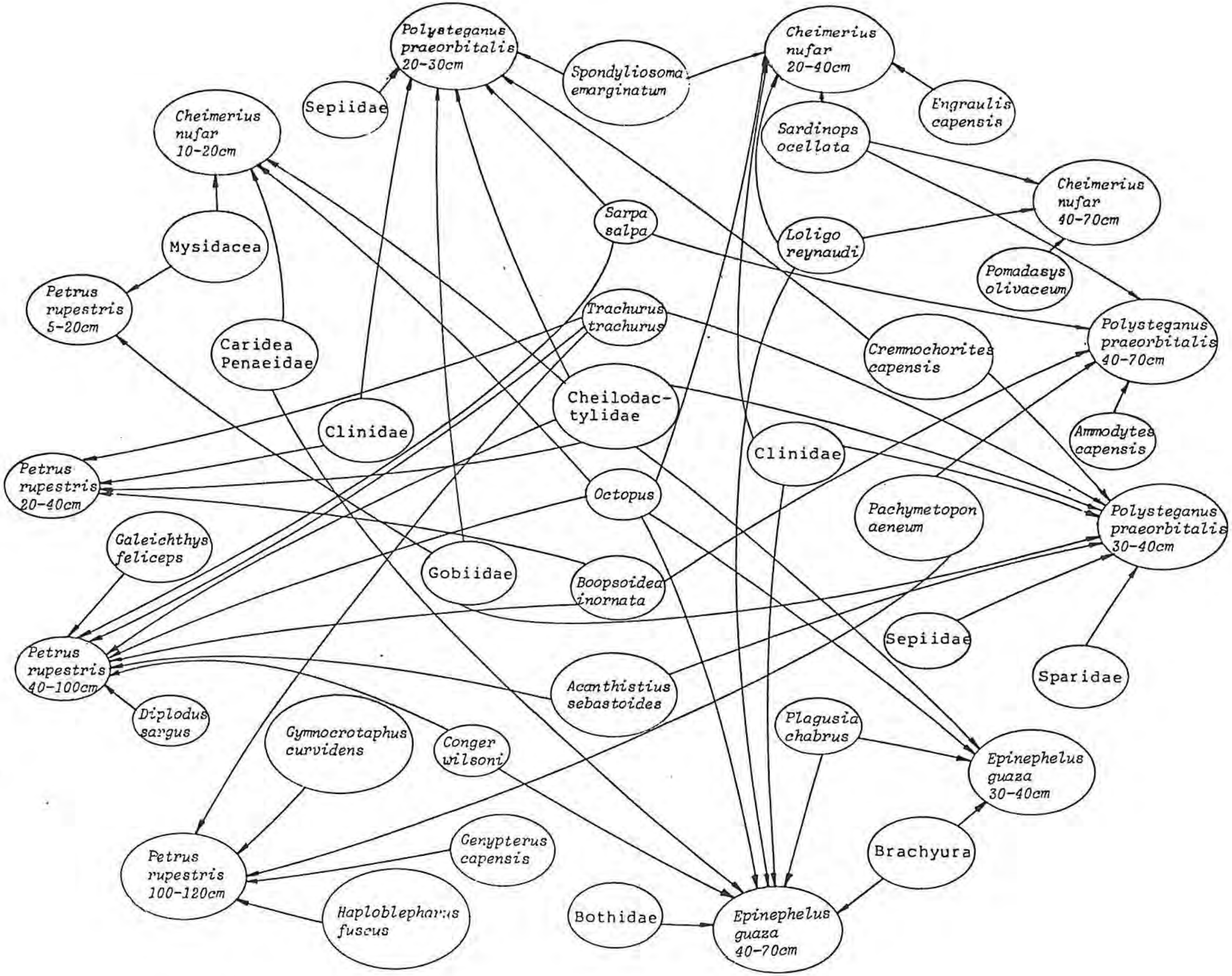


Fig. 73. The food web of coastal reef fishes in the eastern Cape. Prey making up more than 4% by mass of the predators stomach contents are shown.

the food web, and more extensive data of predatory interactions have been collected. It seems likely that a similar dependence of a wide range of predators on relatively few prey will be found when studies on other top carnivores are initiated in the eastern Cape.

Natural mortality resulting from predation on the key prey species is clearly high at all stages of the prey's life cycle. Although it is premature to assume that there is competition for prey, this aspect merits some attention. It is particularly important in the western Cape where a large pelagic fishery has had a detrimental effect on the seabird population (Crawford & Shelton 1978, Furness & Cooper 1982) and also presumably on pelagic fish predators. The eastern Cape does not have a pelagic purse seine fishery and the Bird Island (Algoa Bay) gannet colony is showing signs of increase (Randall & Ross 1979). As these gannets feed on S. ocellata, E. capensis and other pelagic fishes, it seems that prey is not a limiting factor and hence competition for food recources may not be occurring. This is merely inferred, however, and still needs to be substantiated.

The food web of top reef predators is characterised by a similar or greater number of prey species than the inshore pelagic system (Fig. 73), although the diversity of prey taken by reef carnivores in this region is lower than in tropical areas (Hiatt & Strasburg 1960, Randall 1967). This is undoubtedly a reflection of the lower diversity which is characteristic of temperate regions (Ekman 1967, McArthur 1972). Although diversity is known to be greater in the tropics than in temperate regions the causes are still debated (Odum 1971, MacArthur 1972, Krebs 1978). Predation has been shown to have an influence (Paine 1966) in intertidal studies. This has yet to be confirmed in marine fishes. Emery (1978) hypothesised that the species richness of fishes is inversely related to the degree of climatic perturbation and is directly related to the amount of solar radiation, availability of nutrient supply, area and availability of cover. He notes that the availability of cover affects both predation and competition. Furthermore, he notes that it is typical to find a greater diversity in near-reef environments than in pelagic regions. The findings made in the present study appear to confirm this generalization.

Among the Sparidae there was a clear ontogenetic change of prey from small crustaceans to small reef species (e.g. Clinidae) to intermediate sized species (e.g. Cheilodactylidae). The stadia were not clearly defined and prey size varied over the size range of predators. In P. rupestris prey size was more closely related to predator size perhaps because of its strong dentition, gill raker structure and prey choice. Although some important prey (e.g. Cheilodactylidae, Octopus) were shared by several of the reef predators, diving observations suggested that habitat segregation is important among the sparids. This needs confirmation. Apparent segregation could also be accentuated by intense exploitation of those reef fish which may be resident and slow growing. Several studies have found that ecologically similar species are removed relatively quickly by fishing (Potts 1981, Ogden 1982, Randall 1982). Judging by previous reports (Biden 1930), this appears to be the case here and would account for P. rupestris being less common around Algoa Bay than in the Tsitsikamma National Park (pers.obs.). Similarly, E. guaza is rarely observed or caught for the same reason. E. guaza has less overlap with other reef predators on account of its exploitation of large crabs and octopus. Reef fish are of minor importance in their diet over the size range examined, although larger specimens did take fish to a greater extent.

Anatomical and behavioural considerations

Keast & Webb (1966), Keast (1970), Gosline (1971) and Hespenheide (1973) have shown in fishes and other groups that morphology may be used to predict food resource use. This seemed to hold in the present study of top predatory teleosts as body form is characteristic of resource exploitation. The pelagic predators were characterised by forked tails and fusiform bodies. This was found to be most developed in the tunas. The inshore pelagic predator L. amia has a deeper body and well developed dorsal and anal fins which facilitate turning and manoeuvering in the surf zone. The soft bottom demersal predator, A. hololepidotus, on the other hand has a truncate tail and is probably adapted to hunting in dirty water. The reef fish are characterised by deep bodies. The Sparidae have well developed teeth for holding prey while E. guaza has a large mouth and gill covers which allow large prey to be sucked in during an ambush.

The attack strategies of piscivorous fish have been grouped as follows: Those which (1) run down their prey, (2) ambush prey, (3) habituate prey to an illusion that they are non-aggressive or (4) stalk their prey (Hobson 1979). Of the fish described in this study, the tunas, P. saltatrix, L. amia, A. aequidens and S. lalandi belong to the first category. A. hololepidotus and E. guaza belong to the second category while C. nufar, P. rupestris, P. praeorbitalis use a combination of strategies 1,2 and 4. Naturally these are not rigid groups, although for example the tunas and serranids probably suit these categories particularly well. The other species probably use hunting techniques which are more labile and almost certainly vary according to the environment, for example with changes in water turbidity. Because physical features are considerably more changeable in these temperate waters compared to the tropical systems described by Hiatt & Strasburg (1960), Hobson (1972) and Emery (1978), it is likely that predation is less rigid in these temperate waters in terms of time of day, as has been found by Ebeling & Bray (1976). However, the limited time available in this study prevented prolonged and detailed observations of these features. This clearly merits attention in future.

Optimal Foraging

Optimal Foraging Theory is based on attempts to predict food choice (optimal diet), feeding area (optimal patch choice), optimal time to different patches and optimal patterns and speed of movement (MacArthur 1972, Pyke et al. 1977). The usual currency chosen in studies is energy and the outcome is thought to optimise fitness (Pyke et al. 1977, Hughes 1980). This theory was used in a study of optimal swimming speed, growth and metabolism by Ware (1975). Although not a part of the current programme, some of the questions raised by this study may be resolved by such an approach. For example, the difference in feeding behaviour between C. nufar and P. rupestris is probably related to their habitat use and evaluation of prey. Similarly, the different depths at which A. hololepidotus is found according to size could result from optimal habitat use for finding prey. In the marine environment studies of optimal foraging will probably have to combine field and laboratory studies in order to obtain an understanding of the natural interactions and distributions of predator and prey and to adequately quantify the cost-benefit of exploitation by the predators.

Resource partitioning

Resource partitioning among members of natural communities has received much attention. The theory has developed from the writings of Darwin (1906) and the mathematical treatments of Lotka and Volterra (in Maynard Smith 1974) and Crombie (1947). Recent studies on natural communities include the work of Pianka (1973, 1974), Alevizon (1975), Werner et al. (1977) and Targett (1981).
Competition for limited resources is generally believed to have forced species to use resources in a different way (Ross 1977). Sale (1979), however, noted that competition exists only when the requirements of two or more individuals for a particular resource exceed supply of that resource in the place where they are living, or that they interfere with one another in their joint efforts to obtain the resource. This definition agrees with that of Larkin (1956) and Birch (1957). MacArthur (1972) has observed that competition for food (for example) may occur only infrequently but may still have a profound influence on bird distribition. Similarly Zaret & Rand (1971) produced evidence suggesting that competition between tropical stream fishes may be intense during the dry season with limited prey availability but that more food overlap is found in the wet season when prey are abundant. They suggest that their data provides strong support for the competitive exclusion principle.

Schoener (1974) reviewed resource partitioning studies and made five generalizations. The first, was that habitat dimensions are important more often than food-type dimensions, which are important more often than temporal dimensions. The results of this study will be reviewed briefly to determine if they conform to this generalization.

The separation of the predatory groups according to habitats - pelagic, soft-bottom demersal and reef fish - confirms this observation although it needs qualification. The predator groups do feed according to habitat but there is some overlap. For example the inshore pelagic fish, P. saltatrix and L. amia, hunt in mid-water and take pelagic prey but demersal fish are also taken. This is partly because they inhabit inshore water and in shallows the distinction between pelagic and demersal is not always clear, as has also been observed by Whitfield & Blaber (1978). On the other hand, tuna feed exclusively on pelagic prey mainly because their bodies, highly adapted for swimming in open water, (e.g. Collette 1978 and see Chapter 4) are not suited for rapid turning or hunting in spatially complex environments. Similarly reef fish and soft-bottom demersal predators also took pelagic prey or fish normally associated with other environments. The fish usually inhabit their characteristic habitats but may be seen in other areas. A. hololepidotus may thus be seen over sand or reef and P. rupestris also swims over sand between reefs. In summary, the habitat choice of these fish is not rigid but certain areas are strongly preferred. The preference is strongest in highly adapted species, such as tunas, rock cod and red steenbras.

Subdivision of habitat was also observed in this study. This often occurs when an abundant species has different depth preferences with increasing size. Examples are A. hololepidotus which prefers shallow water when small and P. rupestris, which uses offshore banks when adult. Similarly, it was suggested that A. hololepidotus uses shallower soft substrates than Merluccius capensis. From this discussion it appears that habitat use is important in such top predatory teleosts. Other workers have also suggested that habitat use is important in fish communities (Larkin 1956, Zaret & Rand 1971, Mendelson 1975, Engel & Magnuson 1976, Werner et al. 1977, Keast et al. 1978, Keast 1978). In marine studies, similar findings have been made by Smith & Tyler (1972), Davis & Birdsong (1973), Harmelin-Vivien & Bouchon (1976) and Ebeling & Bray (1976). Alevizon (1975) has demonstrated that the division of spatial resource is greatest between surf perches which take similar prey but that overlap is greatest between congeners which differ markedly in diet.

Partitioning of food resources was illustrated using two similarity analyses. Those pelagic predators taking highly abundant engraulids and clupeids were most similar inshore while offshore tunas partitioned resources more effectively and took different prey, as predicted by Magnuson & Heitz's (1971) work on gill rakers. Intraspecific food resource partitioning results from behavioural and morphological differences. For example, the marked selection for squid by large S. lalandi probably results from preferred hunting areas. Large P. saltatrix differed in their prey selection because they school less and consequently are less efficient at attacking schooled prey, as has been found for other fish (Major 1977 and Chapter 4). The lower trophic similarity between reef predators, as was seen by the low level of linking suggests greater partitioning.

Partitioning by prey size was shown here and has been documented in several other studies (e.g. Ross 1977, Werner et al. 1977, Angermeier 1982). Juveniles generally took smaller prey. This results in small predators of different species taking similar sized prey (for example crustaceans of up to 20 mm and larval fishes) while the largest predators commonly take prey up to 200 - 300 mm or larger. The size of prey selected appeared to depend on availability and abundance. For example, yellowfin tuna over the entire size range studied will take engraulids of about 100 mm or pilchards of 200 mm when abundant. In all species examined the large predators had a wide range of preferred prey and the maximum prey size taken varied according to prey species. Elongate eels, for example, were taken while deeper-bodied prey of the same size could not have been ingested. Since these predators were all top carnivores, the upper prey size available to them was similar, although P. rupestris particularly took very large fish which would not have been available to most of the predators. Interspecifically, segregation by prey size seemed less important than prey species selected (see also Angermeir 1982). Interestingly, juveniles of top predatory species may potentially be competing with each other as well as with smaller species lower in the food web. This may have a profound effect during exploitation when the age structure of populations is decreased. Ogden (1982) has noted that the effects of continuous removal of certain parts of the fish community, as occurs with the fishing, are not understood.

No information was collected on temporal partitioning apart from stomach content analyses and diving observations. These observations showed that the predators appeared to be at least diurnal. Studies by Hobson (1968, 1974) and Major (1977) have shown that feeding time may be important in some species. This does not appear to hold in temperate kelp beds (Ebeling & Bray 1976) and Stark & Davis (1966) suggest that it may be unimportant in many species of large predators. The diurnal feeding patterns of these top predators in the eastern Cape need further research. Seasonal occurrence of tunas in inshore waters may be related to movement of schools of clupeids and engraulids. This also needs confirmation before conclusions on the use of inshore waters by tuna can be fully understood. It was hypothesized, however, that eastern Cape coastal waters are important feeding grounds for several pelagic species between breeding seasons (Chapter 4).

In conclusion, it appears that habitat use and food selection are interrelated in top predatory teleosts. As these fishes are highly mobile, it is not easy to separate habitat and prey use to determine which is most important in resource partitioning in these predators. The two extremes of habitat and prey partitioning are characterised by tunas as compared to reef fish, particularly rockcod and red steenbras. Many of the other species exhibit varying degrees of resource sharing of both resource dimensions. Although limited information is available on temporal dimensions, these appear to be of lesser importance to top predatory teleosts.

Keast (1979) noted that top predatory teleosts are specialists - do the findings in this study confirm this? To investigate this the diet of each group was analysed using the Shanon-Wiener diversity index in which the number of species and evenness of allotment is quantified using log base 2 (Krebs 1978). Number and mass contributions are shown but mass is preferred as number is subject to bias of small crustaceans which tend to swamp other prey (Table 30). The increasing diversity offshore of Cape Recife and at East London of *T. albacares* and *K. pelamis* suggests that the diversity of prey taken may be a function of the diversity of prey available. The similarity of the fish taken by kob of 501 - 1000 mm compared to trawl data confirms this. The range of diversity indices is lower than intertidal trawl stations (Lasiak 1982), suggesting that although these predators are generalists they only take some of the available prey. Not only do the values vary between predators but they change with growth. The low value recorded for *Seriola lalandi* larger than 700 mm is a reflection of it taking the squid *L. reynaudi* dominantly. Lasiak (1982) has shown how diversity fluctuates through the year in the surf zone of Algoa Bay. This too, would affect the diversity index of prey taken, low values being recorded when highly abundant prey are taken

Table 30. Shanon-Wiener diversity indices of prey taken by each predator size-group. The indices of number and wet mass are presented. Values for *A.hololepidotus* of 50-100 cm and the *T.B. Davie* Trawl data are presented by number. Measurements are in cm.

	A) Prey number				B) Prey mass			
Length range (cm)	40-60	60-80	80-140		40-60	60-80	80-100	
T. albacares I.	2.13	2.16	2.41		2.16	1.68	1.87	
T. albacares O.	2.6	2.69	2.22		2.42	2.84	1.96	
T. albacares EL.	3.35	2.71	2.90		2.56	2.87	2.77	
Length range (cm)	40-50	50-60	60-70		40-50	50-60	60-70	
K. pelamis I.	-	1.42	0.29		-	1.45	0.06	
K. pelamis O.	0.26	0.21	2.05		2.1	2.81	2.13	
K. pelamis EL.	2.67	3.56	2.34		2.52	2.49	1.11	
Length range (cm)	40-70	70-120			40-70	70-120		
L. amia	2.6	2.85			2.71	2.69		
Length range (cm)	10-30	30-40	40-50	50-70	10-30	30-40	40-50	50-70
P. saltatrix	1.29	2.59	2.84	2.73	2.64	2.44	2.80	2.37
Length range (cm)	40-70	70-130			40-70	70-130		
S. lalandi	3.4	1.6			3.32	1.67		
Length range (cm)	30-60	60-100			30-60	60-100		
A. aequidens	2.52	2.79			2.46	1.77		
Length range (cm)	20-30	30-50	50-100	100-180	20-30	30-50	50-100	100-180
A. hololepidotus	0.06	0.18	0.77	3.41	1.28	3.72	2.99	2.89
Length range (cm)	50-100							
A. hololepidotus	2.16							
T.B.Davie trawl	2.34							
Length range (cm)	10-20	20-40	40-70		10-20	20-40	40-70	
C. nufar	1.48	1.60	2.09		1.86	3.75	1.20	
Length range (cm)	20-40	40-70	70-100	100-130	20-40	40-70	70-100	100-130
P. rupestris	3.46	4.28	3.61	2.52	2.94	3.60	3.21	2.32
Length range (cm)	20-30	30-40	40-70		20-30	30-40	40-70	
P. praeorbitalis	3.29	3.66	3.54		3.03	3.47	2.74	
Length range (cm)	30-40	40-50	50-70		30-40	40-50	50-70	
E. guaza	2.75	3.12	3.18		2.13	2.78	2.70	

and high ones when a variety are eaten. The results agree with Tyler (1972) who noted that although numerous species are taken by marine predators, a much lower number are important. The index shows that reef predators on the whole have higher values than do the pelagic species, showing that either they are more generalised feeders or that a wider diversity of prey is available to them. The comparability of the index depends on good prey identification. The low values in small A. hololepidotus and C. nufar, for example, were probably accentuated by mysids not being identified to species. The use of the term generalist or specialist is limited, however, unless it is possible to make an independent assessment of the quantity and diversity of prey available. Until this is done, the terms are not very meaningful and it is premature to arrive at a definite conclusion.

Applied predator-prey research

The management of multispecies fisheries is complicated by the interaction of component species at different trophic levels. Gulland (1970) states that this can only be resolved with good knowledge of the quantitative relationships between predator and prey including conversion factors of predators consuming prey. We have obviously only begun to determine interlinkages of the trophic system and considerably more needs to be done before these are quantified. Radovich (1979) observes that simplistic models or intuition are both limited for determining the effect on the whole system of manipulating the population of one or two species. He cited the study by Morejohn et al. (1978) as an example which appears to be as complex as the eastern Cape coastal system, as was discussed above.

Even the present state of knowledge will, however, assist in assessing conflicting interests. For example, in the event of anchovy being heavily exploited commercially, it would also be prudent to monitor the bird colonies in Algoa Bay for useful information on fish prey availability (Crawford & Shelton 1978, Batchelor 1982, Furness & Cooper 1982). The population of gannets has recently been shown to be expanding (Randall & Ross 1979) and a marked change in this situation may suggest that man, birds and other predators are competing. This would mean that prey are limited, possibly reducing the migration of gamefish into the area, as has been suggested in False Bay (Nepgen 1982). The present study has shown that the other pelagic predators such as fish would also compete, possibly having a detrimental effect on the commercial line-fishery and sport fishing industry. It would have less direct effect on demersal fishes such as kob, although secondary effects, such as increased predation on juvenile kob by stockfish, are conceivable. Reef fish would probably not be affected although redirected predation may have a negative influence on them.

Predator-prey studies have an important place in fisheries management and the development of ecological theory, as man has a direct effect on the complex and dynamic marine ecosystem. Tody (1979) noted that "management strategies must take into account the interdependence of predator and prey whether it is in ponds ... or in oceans". He also noted, however, that there has been little progress in marine management using predator-prey relationships. It is rarely disputed that marine resources need management, as has been demonstrated by the collapse of the pilchard fishery and reduction of the anchovy catch in the western Cape recently (Crawford & Shelton 1978, Grindley 1979, Crawford 1981a,b). Although management is complicated by political considerations, it seems likely that the development of good predictive models may improve the advice of fisheries biologists. With improved information on predator-prey relationships (which would necessitate experimental manipulations), and a better understanding of the distribution and biology of interacting species, the development of such models will be possible. Models based on adequate biological information could also be used to investigate the effect of removal of large predators from the ecosystem to understand how this effects the food web (Ogden 1982). They may also resolve whether the presence of several top predators is essential for the present level of diversity of fishes in the tropics (Ogden & Ebersole 1981) and in warm temperate waters, as Paine (1966) has already established for invertebrates in the intertidal zone.

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Appendix Table 1. A complete list of prey recorded from the predators in this study.

Polychaeta	
Crustacea	
Copepoda	
Isopoda	
Stomatopoda	
Mysidacea	
Mesopedopsis slabberi	von Beneden 1861
Mysidopsis sp.	
Euphausiacea	
Natanita	
Cardiaea	
Penaeidea	
Macropatasma africanum	(Balss 1913)
Brachyura	
Megalopa larvae	
Plagusia chabrus	(Linnaeus 1758)
Pseudodromia sp.	
Macrura	
Scyllarides elisabethae	(Ortann 1894)
Anomura	
Callianassa sp.	
Mollusca	
Gastropoda	
Pteropoda	
Cephalopoda	
Sepiidae	
Teuthoidea	
Loliginidae	
Loligo reynaudi	Orbigny 1845
Lycoteuthidae	
Lycoteuthis diadema	(Chun 1900)
Enoploteuthidae	
Abralia spp.	
Abraliopsis sp.	
Ommastrephidae	
Thysanoteuthidae	
Thysanoteuthis sp.	
Chiroteuthidae	
Onychoteuthidae	

Cranchidae	
Octopoda (Pelagic)	
Ocythoe sp.	
Argonauta spp.	
Tremoctopus violaceus	Delle Chiaje, 1830
Octopoda (Benthic)	
Octopus vulgaris	Cuvier 1798
Ophiuroidea	
Chondrichthyes	
Haploblepharus fuscus	Smith 1950
Osteichthyes	
Gonorynchidae	
Gonorynchus gonorynchus	(Linnaeus 1766)
Clupeidae	
Etrumeus teres	(Dekay 1824)
Sardinops ocellata	(Pappe 1853)
Engraulidae	
Engraulis capensis	(Gilchrist 1913)
Ariidae	
Galeichthys feliceps	(Valenciennes 1840)
Myctophidae	
Diaphus sp.	
Exocoetidae	
Cypselurus sp.	
Hemirhamphus sp.	
Hyporhamphus sp.	
Oxyporhamphus sp.	
Scomberesocidae	
Scomberesox saurus	Fleming 1823
Belonidae	
Petalichthys capensis	Regan 1904
Bregmacerotidae	
Bregmaceros sp.	
Merluccidae	
Merluccius capensis	Castelnau 1861
Ophidiidae	
Genypterus capensis	(Smith 1847)
Congrogadiidae	

Halidesmus scapularis	Günther 1871
Bothidae	
Soleidae	
Astroglossus pectoralis	(Kaup 1858)
Cynoglossidae	
Cynoglossus capensis	(Kaup 1858)
Cynoglossus zanzibarensis	Norman 1939
Ammodytidae	
Ammodytes capensis	Barnard 1927
Cheilodactylidae	
Cheilodactylus fasciatus	Lacepede 1803
Cheilodactylus pixi	Smith 1980
Chirodactylus brachydactylus	(Cuvier 1830)
Priacanthidae	
Priacanthus sp.	
Priacanthus cruentatus	(Lacepede 1802)
Serranidae	
Acanthistius sebastoides	(Castelnau 1861)
Apogonidae	
Carangidae	
Trachurus trachurus	Castelnau 1861
Pomatomidae	
Pomatomus saltatrix	(Linnaeus 1766)
Scombrops dubius	Gilchrist 1922
Sciaenidae	
Argyrosomus hololepidotus	(Lacepede 1802)
Umbrina canariensis	(Valenciennes 1843)
Pomadasyidae	
Pomadasys olivaceum	Day 1875
Rhonciscus striatus	(Gilchrist & Thompson 1908)
Sparidae	
Argyrozona argyrozona	(Valenciennes 1830)
Boopsoidea inornata	Castelnau 1861
Cheimerius nufar	(Ehrenberg 1830)
Diplodus sargus capensis	Linnaeus 1758
Diplodus cervinus hottentotus	(Valenciennes 1843)
Gymnocroptaphus curvidens	Günther 1859
Lithognathus mormyrus	(Linnaeus 1758)

Pachymetopon aeneum	(Gilchrist & Thompson 1908)
Pagellus natalensis	Steindachner 1902
Polystegnaus undulosus	(Regan 1908)
Pterogymnus laniarius	(Cuvier 1830)
Rhabdopsargus holubi	(Steindachner 1881)
Sarpa salpa	(Linnaeus 1766)
Spondyliosoma emarginatum	(Cuvier 1830)
Scombridae	
Euthynnus affinis	(Cantor 1850)
Scomber japonicus	Houttuyn 1782
Nomeidae	
Cubiceps sp.	
Stromateidae	
Bramidae	
Brama orcini	(Cuvier 1831)
Coryphaenidae	
Coryphaena hippurus	Linnaeus 1758
Mugilidae	
Liza richardsoni	(Smith 1846)
Myxus capensis	Valenciennes 1836)
Atherinidae	
Atherina breviceps	Cuvier 1835
Sphyraenidae	
Sphyraena sp.	
Sphyraena africanum	Gilchrist & Thompson 1909
Gobiidae	
Blenniidae	
Xiphasia setifer	Swainson 1839
Clinidae	
Clinus spp.	
Clinus berrisfordi	Penrith, 1967
Clinus superciliosus	(Linnaeus 1758)
Clinus venustris	Gilcrhsit & Thompson 1908
Pavoclinus spp.	
Pavoclinus laurentii	(Gilchrist & Thompson 1908)
Tripterygiidae	
Cremnochroties capensis	(Gilchrist & Thompson 1908)
Scorpaenidae	

Coccotropsis gymnoderma	(Gilchrist 1906)
Scopaena scrofa	Linnaeus 1758
Triglidae	
Chelidonichthys kumu	(Lesson 1826)
Chelidonichthys queketti	(Regan 1904)
Dactylopteridae	
Dactyloptena orientalis	(Cuvier 1820)
Gobiesocidae	
Chorisochismus dentex	(Pallas 1769)
Congridae	
Conger wilsoni	(Bloch-Schneider 1801)
Baslistidae	
Laputa sp.	
Ostraciontidae	
Ostracion cubicus	Linnaeus 1758
Lactoria sp.	
Tetrosomus sp.	
Diodontidae	
Ciclichthys sp.	
Tetraodontidae	
Lagocephalus sp.	
Molidae	
Batrachoididae	
Chatrabus melanurus	(Barnard 1927)

APPENDIX TABLE 2

Regression values used for calculating prey length and mass in this thesis. Material is stored at the Port Elizabeth Museum and the author used a computer programme written by Dr H.M. Kok to obtainthe regression values. The regression has the form: $y = a.x^b$

	O.L/B.L. - LENGTH				O.L./B.L. - MASS			
Scientific name	a	b	r^2	n	a	b	r^2	n
Sepiidae					0.48	2.568	0.92	B
Loliginidae					7.33	2.8	0.87	C
Loligo reynaudi	58.639	1.009	0.9	A	7.33	2.8	0.87	
Lycoteuthidae							35.5g	B
Lycoteuthis diadema							35.5g	
Enoploteuthidae					2.75	2.8		D
Abralia spp.					2.75	2.8		
Abraliopsis sp.					2.75	2.8		
Ommastrephidae					2.04	2.93		
Thysanoteuthidae					17.4	3.06		
Thysanoteuthis sp.					17.4	3.06		
Chiroteuthidae					1.4	2.83		
Onychoteuthidae					1.78	3.0		
Cranchiidae					2.88	2.28		
Octopoda (Benthic)	10.37	0.98	0.79	122	0.53	2.86	0.74	77
Octopus vulgaris	10.37	0.98	0.79	122	0.53	2.86	0.74	77
Gonorynchus gonorynchus	86.731	1.035	0.97	18	2.0784	3.279	0.96	15
Entrumeus teres	48.056	1.014	0.98	32	0.643	3.193	0.98	34
Sardinops ocellata	48.774	1.137	0.97	50	0.683	3.596	0.97	46

Table continues......

Appendix Table 2 continued:

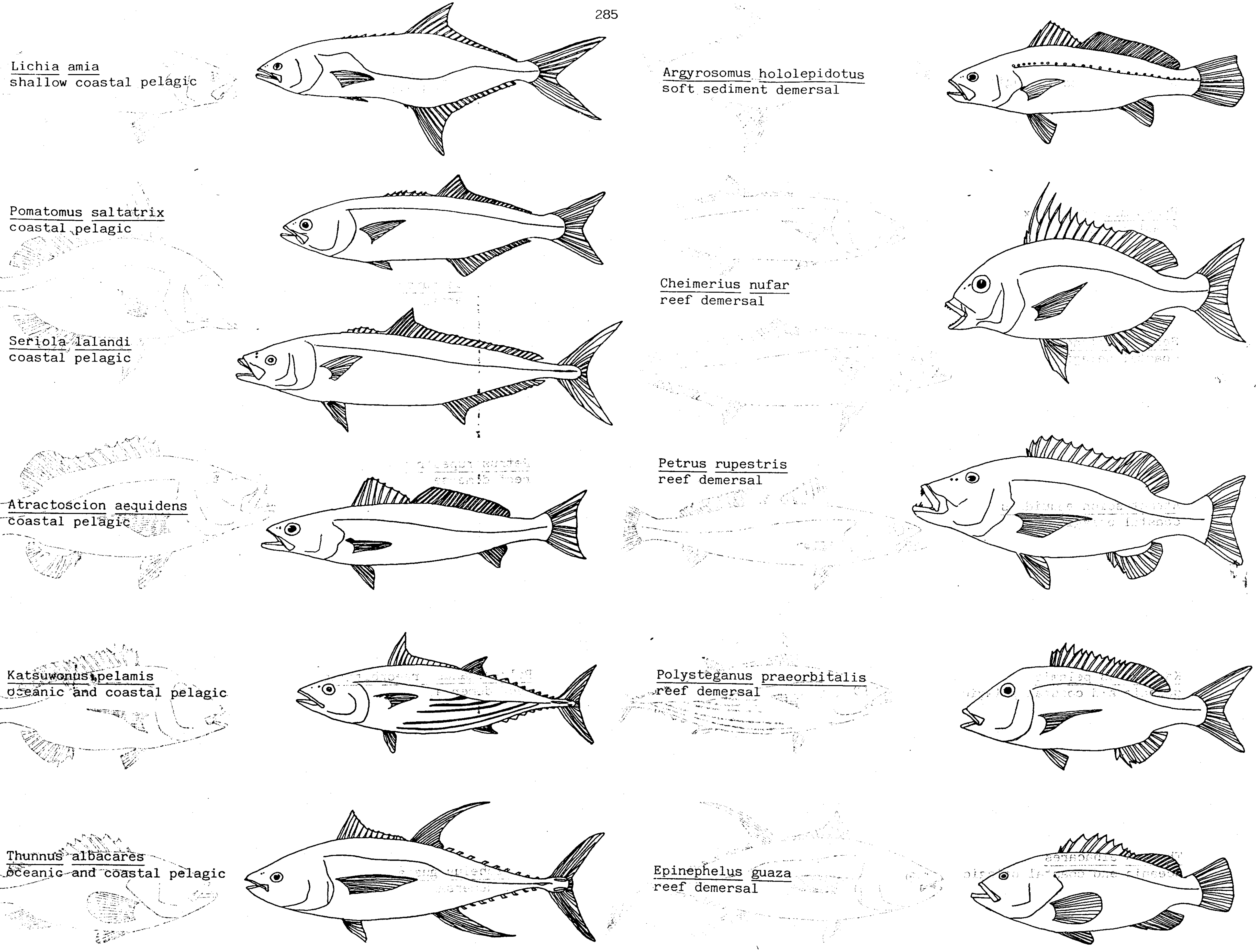
Scientific name	O.L/B.L — LENGTH				O.L./B.L. — MASS			
	a	b	r^2	n	a	b	r^2	n
Engraulis capensis	38.01	0.977	0.98	34	0.331	2.928	0.97	33
Galeichthys feliceps	10.294	1.41	0.98	56	0.0088	4.301	0.98	55
Hemirhamphus sp.	58.411	0.955	0.97	34	0.314	3.109	0.98	34
Hyporhamphus sp.	62.986	0.836	0.91	9	0.2806	2.801	0.77	10
Scomberesox saurus	129.834	1.281	0.94	11	9.251	3.043	0.86	25
Petalichthys capensis	123.47	0.92	0.93	7	1.28	2.95	0.97	7
Merluccius capensis	17.115	1.095	0.98	71	0.025	3.454	0.98	71
Genypterus capensis	13.516	1.482	0.93	10	0.0094	4.505	0.99	9
Halidesmus scapularis	63.979	1.386	0.80	28	0.626	3.399	0.78	28
Austroglossus pectoralis	54.578	1.154	0.95	43	0.581	3.78	0.92	40
Cynoglossus capensis	30.197	1.296	0.97	123	0.136	4.048	0.97	123
Cynoglossus zanzibarensis	30.838	1.393	0.96	38	0.161	4.218	0.96	38
Cheilodactylus fasciatus	31.494	1.273	0.96	25	0.439	3.852	0.98	17
Cheilodactylus pixi	32.733	1.189	0.95	59	0.447	3.741	0.94	60
Chirodactylus brachydactylus	30.936	1.312	0.97	38	0.453	3.792	0.96	30
Priacanthidae	39.577	1.5	0.25	21	1.826	3.78	0.20	19
Priacanthus sp.	39.577	1.5	0.25	21	1.826	3.78	0.20	19
Priacanthus cruentatus	39.577	1.5	0.25	21	1.826	3.78	0.20	19
Acanthistius sebastoides	15.302	1.167	0.98	55	0.063	3.53	0.99	53
Trachurus trachurus	28.812	1.007	0.98	66	0.232	2.915	0.98	71
Pomatomus saltatrix	16.948	1.292	0.97	87	0.040	3.91	0.98	87
Scombrops dubius	19.435	1.098	0.99	9	0.080	3.267	0.99	7
Argyrosomus hololepidotus	11.325	1.356	0.98	122	0.014	4.035	0.98	122
Umbrina canariensis	14.885	1.225	0.97	135	0.036	3.755	0.98	141
Pomadasys olivaceum	16.167	1.1	0.99	97	0.061	3.294	0.97	103

Table continues.......

Appendix Table 2 continued:

Scientific name	O.L./B.L.	LENGTH			O.L./B.L.	MASS		
	a	b	r^2	n	a	b	r^2	n
Pavoclinus laurentii	81.135	1.338	0.84	26				
Tripterygiidae	20.231	1.171	0.94					
Cremnochorties capensis	20.231	1.171	0.94	14	0.108	3.599	0.92	14
Coccotropsis gymnoderma	22.25	0.93	0.97	26	0.197	2.941	0.94	26
Chelidonichthys kumu	36.442	1.39	0.96	13	0.495	4.128	0.94	12
Chelidonichthys queketti	49.2	1.224	0.97	10	0.97	3.749	0.97	10
Conger wilsoni	58.344	1.316	0.92	7	0.188	4.267	0.92	7
Chatrabus melanurus	22.82	1.08	0.99	3	0.13	3.47	0.95	3

A From Batchelor A.L.B. (pers.comm.): B From Ross (1979): C From Cooper (1979): D Modified from Clarke (1962) for power curve and measurements in mm.



Lichia amia
shallow coastal pelagic

Pomatomus saltatrix
coastal pelagic

Seriola lalandi
coastal pelagic

Atractoscion aequidens
coastal pelagic

Katsuwonus pelamis
oceanic and coastal pelagic

Thunnus albacares
oceanic and coastal pelagic

Argyrosomus hololepidotus
soft sediment demersal

Cheimerius nufar
reef demersal

Petrus rupestris
reef demersal

Polysteganus praeorbitalis
reef demersal

Epinephelus guaza
reef demersal

Fig. 3. Important top predatory teleosts of coastal waters of the eastern Cape. Fold out for easy reference.

ERRATA

Page	Para.	Line	Error	Correction
i	-	-	Title	Resource partitioning by top predatory teleosts in eastern Cape coastal waters (South Africa).
1	1	11	Lasaik	Lasiak
2	3	10	albares	albacares
9	2	2	was	...entire catch of each was sorted.
13	1	21	pi	P_i
16	4	1	schoolng	schooling
28	5	1	As	A total...
18	-	-	Macropatsma	Macropetasma
23	-	-	Macropatsma	Macropetasma
35	5	4	a lot	many
9	1	6	prepared	adapted
9	1	7	adaptation	light compensation
54	1	5	observatioons	observations
43	3	3	reyanudi	reynaudi
62	2	2	particulary	particularly
79	1	6 & 7	...dumping...	...difficulty shedding excess heat.
82	5	4	megalopa larvae	megalopae. This should be replaced throughout.
100	2	24	indiates	indicates
101	2	6 & 9	Ommastrephidae	Ommastrephidae
103	3	2	covergent	convergent
104	3	2	retia mabila	retia mirabilia
110	3	1	or	on
125	3	2	occurence	occurrence
146	Fig 41	-	-	Open bars with arrows are ∞
154	4	3	'(Oy)'	(O + y)
155	1	1	O years	O + years
157	2	1	interpertations	interpretations
160	3	5	Saaman	Saayman
164	3	7	Hoogeland	Hoogland
166	2	2	Fig 3.	Fig 3).
166	2	8	largely	large
180	3	8	patter	pattern
181	1	1	O-1	O+-1
181	2	13	crustacea	Crustacea
221	3	5	low	slow
223	2	7	Regeier	Regier
223	2	9	competiton	competition
225	2	4	diplayed	displayed
226	3	5	species genera	species, genera
229	2	6	adequatly	adequately

Page	Reference	Error	Correction
250	Baird (1971)	occurence	occurrence
251	Bigelow & Schroeder (1953)	Widl.	Wildl.
251	Blaber (1973)	Popoulation	Population
252	Blaber (1974)	Juveniles	Juveniles of
252	Blaber (1974)	Fish.	Fish
252	Buchan & Smale (1981)	consuption	consumption
253	Carey et al. (1971)	11	11
253	Clarke (1972)	shale	whale
254	Clarke et al. (1979)	buyoyancy	buoyancy
254	Collette & Talbot (1972)	Cty.	Cty
254	Cott (1957)	Mathuen	Metheun
258	Graham & Diener (1978)	Diener	Diener, D.R.
258	Hartline et al. (1972)	Harline P.H.	Hartline, P.H.
258	Hartline et al. (1972)	Cty.	Cty
258	Hartline et al. (1972)	Chromis cyaneus	Chromis cyaneus
259	Heydorn et al. (1978)	resonses	responses
259	Hobson (1979)	predator-prey	Predator-prey
260	Holme (1974)	Mollusca...	(Mollusca...
261	Kayes (1974)	is	in
261	Keast (1970)	bioernergetic	bioenergetic
261	Keast & Harker (1977)	Keast, A., Harker	Keast, A. & Harker
261	Kok et al. (in prep)	etuarine	estuarine
261	Lasiak (1981)	Nursary	Nursery
262	Magnuson (1978)	-hydromechanis	-hydromechanics
263	Magnuson & Heitz (1971)	Mackjerels	Mackerels
263	Major (1978)	Anim. Behr.	Anim. Behv.
263	Medved & Marshall (1981)	Sandbars	Sandbar
264	Morejohn et al. (1978)	apsects	aspects
265	Norman & Greenwood (1963)	Norman, J.T.	Norman, J.R.
265	Norris & Dahl (1980)	Catecean	Cetacean
265	Odgen (1982)	Stated	States
265	Orions (1971)	Acamdemic	Academic
266	Partridge (1982)	Patridge	Partridge
266	Penrith (1972)	Zoologica Afr.	Zool. afr.
266	Perrin et al. (1973)	porpose	porpoise
266	Popper & Fishelson (1973)	Fischelson	Fishelson
266	Porumb (1968)	salatrix	saltatrix
266	Potts (1970)	Aldavera	Aldabra
266	Potts (1980)	Aldabora	Aldabra
267	Rand (1960)	distribition	distribution
267	Randall (1982)	Procedings, Octover	Proceedings, October
267	Randall & Randall (1978)	roseati	roseate
267	Randall et al. (1981)	algoa	Algoa
268	Regier et al. (1979)	Regeir	Regier
268	Richard (1969)	low-frquency	low-frequency
268	Sale (1979)	Wachington	Washington
269	Smale (1978)	Panulinus	Panulirus
270	Stein (1977)	forgaging	foraging
271	Talbot (1955)	Rhabodosargus	Rhabdosargus
271	Treisman (1975a)	Concelement	Concealment
271	Treisman (1975b)	Triesman	Treisman
271	Tody (1979)	Untilization, systemas	Utilization, systems
272	van der Elst (1976)	costal	coastal
272	Vaughan & Recksiek (1978)	acouctic	acoustic
272	von Frisch (1938)	Naturwissenschafter	Naturwissenschaften
272	Wallace & van der Elst (1975)	esturine	estuarine
274	Yabe et al. (1963)	distribituion	distribution
274	Yabe et al. (1963)	eggs; larvae	eggs, larvae
274	Zaret & Rand (1971)	competative	competitive
278		Polystegnaus	Polysteganus
278		Rhabdopsargus	Rhabdosargus
278	Clinus venustris	Gilcrhsit	Gilchrist
278		Cremnochroties	Cremnochorites
279		Scopaena	Scorpaena
279		Baslistidae	Balistidae
279		Ciclichthys sp.	Cichlichthys sp.
282		Gymnocroptaphus	Gymnocrotaphus
283		Cremnochorties	Cremnochorites
284			Total length is used for Argyrosomus hololepidotus and Epinephelus guaza