TROPHIC RELATIONSHIPS IN JUVENILES OF THREE SPECIES OF SPARID FISHES IN THE SOUTH AFRICAN MARINE LITTORAL

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ABSTRACT

The feeding habits of three sparids, *Diplodus sargus, D. cervinus,* and *Sarpa salpa,* were studied. Juveniles of these fishes occur commonly in the intertidal and immediately subtidal regions of southeast Africa, while adults were only observed in these zones at high tide. Small juvenile *D. sargus* feed largely on harpacticoid copepods, amphipods, and, in spring and early summer, cirripede nauplii, chironomid larvae, and an unidentified trochophore larva. Larger individuals mainly take amphipods and green algae. Successive size classes of *D. cervinus* feed mainly on harpacticoid copepods and chironomid larvae, the shrimp *Palaemon pacificus,* amphipods, and then polychaetes. *Sarpa salpa* ingest harpacticoids when small, diatoms and red algae as a large juvenile, and red and green algae as an adult. Corresponding changes in gut length and dentition are reported for *S. salpa.*

Marked ecological separation of the three species was observed. Small juveniles appear at different times of the year and feed on different foods (dietary and temporal separation). Larger juveniles and subadults have different diets or feed in separate parts of the littoral zone (behavioral, dietary, and spatial separation).

A brief review of methods of analyzing stomach contents is included and it is suggested that a combination of points and ranking indices would be the most valuable. The method, here termed the comparative feeding index, is described.

The food and feeding relationships of fishes in the intertidal zone of South Africa are poorly documented and the results are largely qualitative. The most important of these studies deal with one or two species of the families Gobiidae (Pitt-Kennedy[2]), Sparidae (Hutchings[3]), Cheilodactylidae (Butler[4]), and Gobiesocidae (Stobbs[5]).

Three species of sparids were investigated in the present survey, *Sarpa salpa* (Linnaeus 1758), *Diplodus sargus* (Linnaeus 1758), and *D. cervinus* (Lowe 1838). Barnard (1927), Smith (1965), and Hutchings (see footnote 3) described *S. salpa* (strepie) as being primarily a herbivore, whereas Talbot (1954) found the fish to be omnivorous. The latter study was made in an estuary, however, where algae are generally less abundant than in the intertidal region. *Diplodus sargus* (blacktail) is described as being an omnivore (Biden 1954; Talbot 1954; Smith 1965), as is *D. cervinus* (zebra). Little, however, has been published on the food and feeding habits of the juveniles of these three species, although they are abundant in the intertidal and immediately subtidal regions of this coast.

The objectives of this study have, therefore, been to determine: 1) the diet of juveniles of these three species; 2) how feeding changes with age and season; 3) the degree of overlap between species, possibly resulting in competition; 4) recruitment times and approximate growth rates of the fish; and 5) the relationship between dentition, gross gut morphology, and diet.

During the course of this study, existing methods of fish feeding analysis were found to be inadequate and a new technique is described which overcomes some of the problems.

MATERIALS AND METHODS

Fish were collected from February to December 1975 at 2-wk intervals during spring tide, in spite of the possibility of introducing biases, as diving

[1]J. L. B. Smith Institute of Ichthyology, Rhodes University, P.O. Box 94, Grahamstown, 6140, South Africa.

[2]Pitt-Kennedy, S. 1968. A preliminary investigation of feeding in two gobies *Coryphopterous caffer* (Günther) and *C. nudiceps* (C. and V.) with notes on their sexual maturity. Unpubl. honors proj., 39 p. Zool. Dep., Univ. Cape Town, S. Afr.

[3]Hutchings, L. 1968. A preliminary investigation into the diets of two littoral teleosts, *Sarpa salpa* (Linnaeus) and *Pachymetopon blochii* (Valenciennes), with notes on their biology. Unpubl. honors proj., 25 p. Zool. Dep., Univ. Cape Town, S. Afr.

[4]Butler, G. S. 1975. An investigation into the biology of two inter and infratidal species of Cheilodactylidae (Pisces: Teleostei). Unpubl. honors proj., 29 p. Zool. Dep., Rhodes Univ., Grahamstown, S. Afr.

[5]Stobbs, R. E. In preparation. Preliminary investigations into the feeding behaviour and food preferences of *Chorisochismus dentex* (Pisces: Gobiesocidae).

Manuscript accepted August 1977.
FISHERY BULLETIN: VOL. 76, NO. 2, 1978.

conditions were most suitable at this time. Hand nets were used in the intertidal pools and multiprong spear guns in the subtidal area. Hook and line, poison, traps, and gill nets were not used as further biases may be induced to the feeding data (Randall 1967). Fish collected with hand nets were immediately placed in a 10% Formalin[6] solution, whereas this procedure was delayed for up to 1½ h in the case of those taken by spear. It was concluded that death stops or greatly slows digestion, as the stomach contents were found to be in an equally digested state in both groups on later analysis. This has also been observed by Hobson (1974).

The fish were left in Formalin for 10 to 14 days. This time period was maintained throughout to standardize any length and weight changes induced by the fixative (up to 5%, Royce 1972). About 10 scales were removed from under the pectoral fin and cleaned with a camel hair brush after having been soaked overnight in water with a trace of carbolic acid (Pinkas 1966). They were mounted dry and examined over a white background using a low-power binocular microscope. Standard lengths to the nearest millimeter were taken and the stomach removed and placed in 45% n-propyl alcohol.

The stomach is here defined as that part of the gut between the last gill arch and the gut caecae. The intestines were not examined as some food items are more resistant to digestion than others, with resultant biases as one moves along the gut (Randall 1967; Kionka and Windell 1972; Gannon 1976). Food items were identified to species where possible.

Numerous methods have been employed in analyzing the food habits of fishes and volumetric and gravimetric techniques are being more widely used today with the current trend towards greater accuracy (Windell 1971). Both suffer from the same limitation in that digestion of the food both reduces its volume and weight. This has resulted in the use of reconstructed weights and volumes where the live weight and/or volume is back-calculated from a measureable parameter, e.g., carapace length (M. Bruton, pers. commun.). In this particular study some of the fish had fed on diatoms and it is not feasible to determine the volume of such small items (Windell 1971). Similarly, the reconstructed weight could not be determined as a sample of monospecific, uncontaminated diatoms is impracticable to obtain and contains an indeterminate number of dead frustules which varies from sample to sample (Round 1971).

In such cases, the points (Swynnerton and Worthington 1940) and ranking index methods (Hobson and Chess 1973) would appear to be more satisfactory and were initially used in the present study. The points system was modified by Frost (1943) and subsequently by Hynes (1950) to take into account gut fullness, 30 points being allotted when the stomach was distended, 20 when full, 10 when half full, and so on. One, two, four, eight, or sixteen points were assigned to each food item rather than fractions of the total allotted to each stomach in proportion to their volumes. This is an artificial situation and the method was revised as described below.

After removal, the stomach is allotted between 0 and 30 points in proportion to its fullness. This is very subjective but overcome to some extent when large numbers of guts are handled. The contents are then sorted, identified, and the percentage volume estimated for each food item with the aid of Data Sheet No. 6 of Geotimes.[7] All estimations are made with the organisms spread out to an even depth throughout the microscope field or equivalent surface. The total number of points allocated to that stomach is then subdivided amongst the food items in proportion to their percentage volumes. The points gained by each food item are summed for the total sample of fish and the mean calculated. The values are then scaled down to a percentage to give the dietary composition of the fish examined. In the case of the ranking index (RI), the volume is estimated as above and the mean calculated for each food item per fish. The mean volume is then multiplied by the ratio of the number of fish containing that item to the total sampled.

The points method, however, places too much weight on single food items that have been fed on to distension by a few fish, whereas the RI method fails to consider stomach fullness. It is therefore suggested that an alternative, here termed the comparative feeding index (CFI), would be more suitable as it takes into account all three factors, i.e., the volume, fullness, and frequency of occurrence of each food item. The method involves the

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Available from the American Geological Institute, 2101 Constitution Avenue, N.W., Washington, D.C.

allotment of points to each food organism as described above and the mean value per fish is then multiplied by the percentage of the total sample of fish that contain that item. As can be seen, the CFI combines the properties of both points and RI methods and thus reduces to some extent the effect of the problems discussed.

The diet of these fish was also determined by the occurrence method (Hynes 1950) as this indicates the feeding preferences rather than the food's volumetric value. This is determined as the percentage of fish in the sample analysed which contain that particular food item.

The dietary composition of *D. sargus* was analysed for the winter (February-July) and summer (August-December) periods, as it was found to be seasonal. This was not done for the other two species, as feeding seasonality is synonymous in these fish with the change in diet with age, as they exhibit discontinuous recruitment.

All skeletal material was cleared and stained using the trypsin maceration, alizarin stain method of Taylor (1967). The gut was dissected out in the same specimens, drawn and measured, and the gut length to standard length ratio (G/S) was calculated as in Weatherly (1972).

STUDY AREA

The study area is situated about 3.2 km north of Kleinemonde in the eastern Cape and is known locally as Clayton's Rocks (Figure 1). The shoreline consists of a gently shelving, sandy beach with broken rocky areas of varying extent.

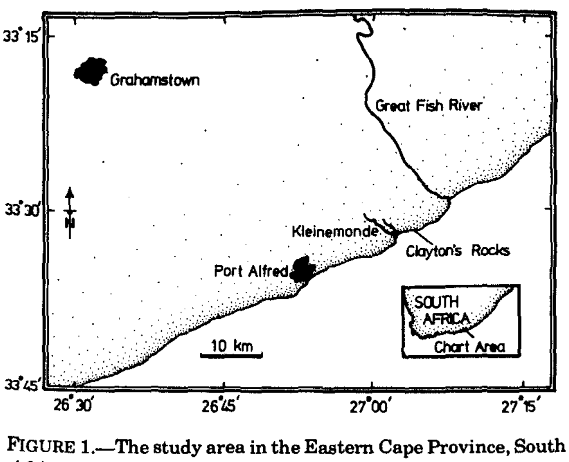

FIGURE 1.—The study area in the Eastern Cape Province, South Africa. Adapted from Topographical Chart 3326, Grahamstown.

The smaller rocky outcrops are continually covered and uncovered by sand, as the beach is unstable and backed by large, shifting sand dunes which move at right angles along the coast. The rocky area under study is made up of sandstone which strikes east-west and dips steeply southwards. This has resulted in the development of gullies and pools partially sheltered from wave action by ridges of resistant rock (Figure 2). The maximum collection depth at the seaward edge of the gullies was 3 m at low tide.

Environmental conditions vary greatly and salinities may fall to 25‰ at low tide, which is caused by freshwater seepage into the pools from springs in the beach. During the day, at low tide, surface water temperatures have been recorded ranging from 26° (summer) to 15°C (winter) in the intertidal and from 22° (summer) to 14°C (winter) in the open sea.

The other major fish species coexisting in the study area are listed below with their general biological characteristics, where known.

ARIIDAE
- *Tachysurus feliceps:* occurs singly, as a juvenile, in crevices.

SPARIDAE
- *Lithognathus lithognathus:* occurs in small groups of juveniles.
- *Rhabdosargus holubi:* juveniles, in small groups.
- *Sparodon durbanensis:* juveniles, observed from October to March, either singly or in small groups.

CHEILODACTYLIDAE
- *Chirodactylus brachydactylus*: as juveniles and subadults, singly, mainly from June to November.

MUGILIDAE
- Unidentified species: occur all year round as juveniles.

CLINIDAE
- *Clinus cottoides*: a purely intertidal species, lives in weed, juveniles appeared about June/July.
- *Clinus superciliosus*: lives in weed, juveniles only observed in November/December.

GOBIIDAE
- *Caffrogobius caffer:* intertidal species, juveniles seen from June to November.

TETRAODONTIDAE
- *Amblyrhyncotes honckenii*: singly or in small groups.

FIGURE 2.—The study site at Clayton's Rocks.

RECRUITMENT AND GROWTH

Diplodus sargus

The monthly and total length-frequency distribution is given in Figure 3. The lumped sample shows a mode in the 10- to 20-mm size class, indicating that larger fish tend to emigrate to deeper water. The juveniles appear in the littoral zone when between 9 and 10 mm standard length (SL), and leave when about 90 mm long. It appears that large fish utilize the intertidal area at high tide as two fish of 107 and 108 mm SL were collected in the intertidal area some 2 h after low tide and another 164 mm long was collected 3 h after low tide.

Visibility was <15 cm in the pools of the research area during September, October, and December due to flooding of the Fish River. No dives could be made during this period in the subtidal area with the result that fish >40 mm were not collected.

Recruitment of the juveniles into the littoral appeared to be relatively constant as no monthly peaks of abundance were found during the survey. This tends to confirm Biden's (1954) suggestion that females of this species spawn throughout the year, though mainly in summer.

No monthly modes could be followed over the period of study as it is a continuously recruiting

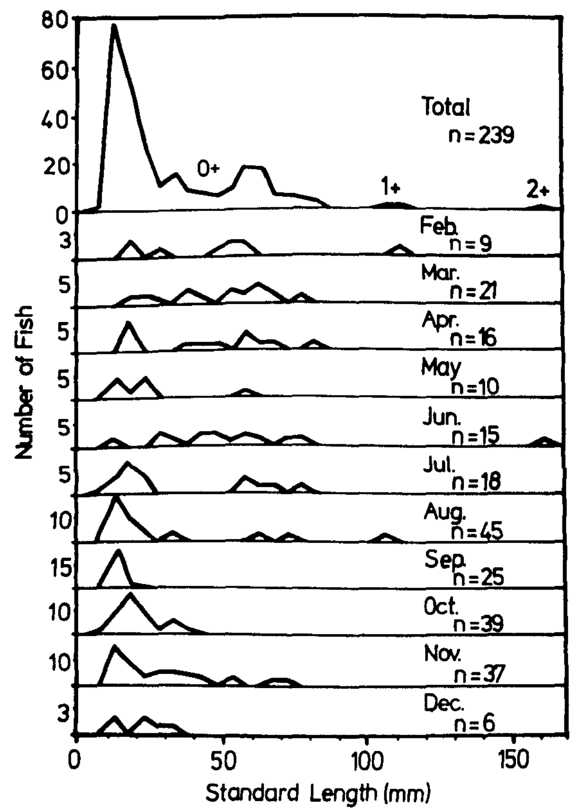

FIGURE 3.—Monthly and total length-frequency distribution of *Diplodus sargus*, showing three age-classes (0+, 1+, and 2+).

population and so growth rates were not estimated. The age of three immature specimens was determined as being 1+ years old (107 and 108 mm SL) and 2+ years old (164 mm SL).

Diplodus cervinus

The length-frequency distribution is given in Figure 4. The total pooled sample shows that this species first appears in the littoral zone when about 8 mm long and leaves again when about 140 mm long. Large fish were observed to move into the intertidal area after low tide, as was the case with *D. Sargus*, but no specimens were obtained.

Monthly modes were observed, which are age-classes 0+, 1+, and 2+ (Figure 4). Recruitment of juveniles into the tide pools is discontinuous, occurring between August and November, with a peak in October. Two fish sampled in August (132 and 129 mm SL) had just formed the second ring, giving the approximate time of scale-ring formation. The estimated average growth rate as determined for mode 1+ is 45 mm from February to December, which is about 54 mm/yr.

Sarpa salpa

The length-frequency distribution shows that the majority of the population is from 9 to 45 mm SL (Figure 5). The juveniles appear in the intertidal when ≥9 mm, and fish >100 mm were never observed in the littoral at low tide; two specimens of age-class 2+ were collected 4 h after low tide.

Three age-classes were observed, labelled as 0+, 1+, and 2+. Recruitment of juveniles into the tide pools is discontinuous, occurring between June and September. Age-classes 1+ and 2+ were approximately ¾ and 1½ yr old, respectively, when sampled. The time of scale-ring formation is then likely to have been about June. The average growth rate is estimated to be 45 mm in 5 mo, or 108 mm/yr for the age-class 0+. Two fish were obtained in April 1976 with lengths of 68 and 76 mm, which indicates that the estimate may be slightly high, the predicted length being 81 mm.

DIETARY COMPOSITION

The composition of the diet is illustrated by occurrence and CFI values scaled down to percentages.

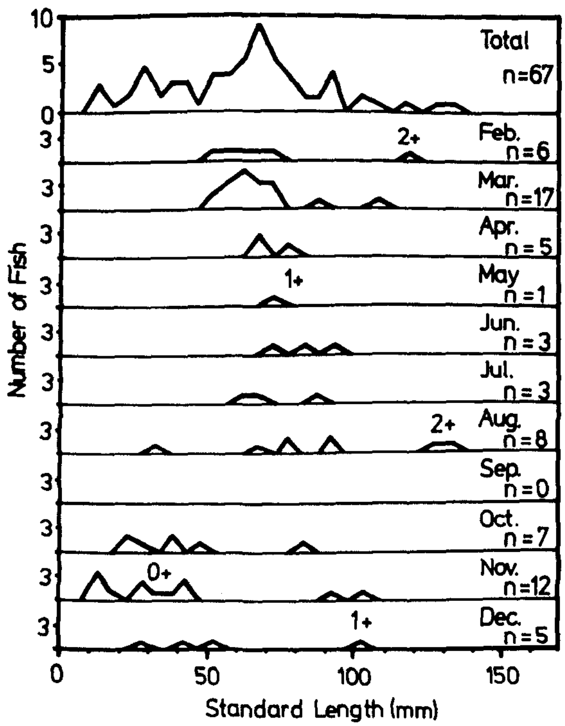

FIGURE 4.—Monthly and total length-frequency distribution of *Diplodus cervinus*, showing three age-classes (0+, 1+, and 2+).

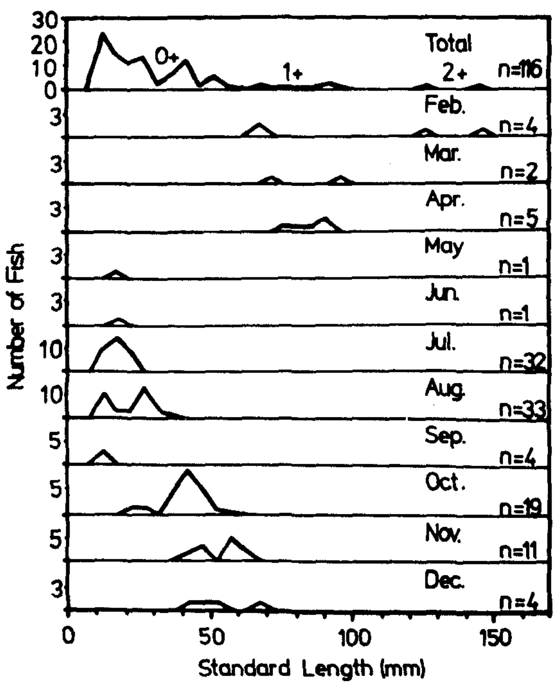

FIGURE 5.—Monthly and total length-frequency distribution of *Sarpa salpa*, showing three age-classes (0+, 1+, and 2+).

Diplodus sargus

Winter Feeding

The diet is composed mainly of harpacticoid copepods, amphipods, algae, isopods, polychaetes, and ostracods (Figure 6; Table 1, n = 88).

The diet of the smallest size class (5-15 mm) is composed almost equally of harpacticoid copepods and amphipods, but the percentage consumed of the former increases in the next size class whereas that of the latter decreases. The diet remained similar in the following two size classes. In the 35- to 50-mm size class, the fish fed little on harpacticoid copepods, the diet being largely composed of amphipods. The situation was similar in the largest size class, although algae and polychaetes were increasingly taken.

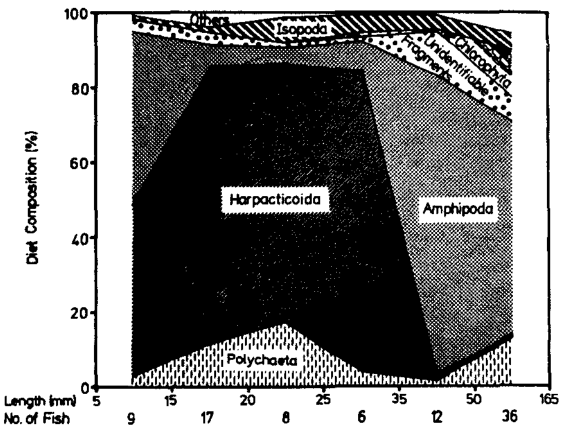

FIGURE 6.—Changes in diet with length of *Diplodus sargus*, collected between February and July 1975, as shown by the comparative feeding index. Food items included in Others are: brachyurans, crab zoaea, diatoms, echinoderms, hydrozoans, leptostracans, molluscs, mysidaceans, *Palaemon pacificus*, rhydophytan algae, sand, and unidentifiable animal fragments.

Summer Feeding

Although similar to the winter diet, chironomid larvae, diatoms, crab zoaea, and leptostracans are more significant. Cirripede nauplii and an unidentified trochophore larva were also commonly taken, and these were not found in winter specimens (Figure 7; Table 2, n = 149).

The diet of the smallest size class (5-15 mm SL) is composed mainly of harpacticoid copepods. The next size class (15-20 mm SL) fed on a similar diet, although the percentage of harpacticoids taken decreased and that of polychaetes and cirripede nauplii increased. These changes were further magnified in the 20- to 25-mm size class. In the next size classes (25-50 mm), there was a change and the green alga, *Ulva* sp., contributed significantly to the diet.

Poor diving conditions in September, October, and December reduced the sample size and only nine fish in the 50- to 165-mm size range were analysed. In general, these fish showed an increasing tendency to take more amphipods, and less

TABLE 1.—Changes in the percentage composition of the food of *Diplodus sargus* with length during the period February to July 1975, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the former, all values exceeding 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)											
	5-15		15-20		20-25		25-35		35-50		50-165	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	—	—	—	—	—	—	1.3	33.3	1.0	25.0	12.8	41.7
Rhodophyta	—	—	—	—	—	—	—	—	0.2	8.3	1.6	16.7
Chrysophyta	—	—	0.2	11.8	—	—	—	—	—	—	0.3	2.8
Polychaeta	2.4	33.3	11.8	76.5	16.7	75.0	3.6	50.0	1.4	33.3	12.8	47.2
Crustacea												
Amphipoda	*47.4*	77.8	5.8	29.4	5.0	25.0	7.8	66.7	*80.1*	66.6	*58.1*	72.2
Ostracoda	0.5	22.2	4.2	58.8	1.2	75.0	0.2	16.7	0.1	8.3	—	—
Harpacticoid copepoda	*45.9*	88.9	*74.2*	82.4	*69.3*	100.0	*80.9*	66.7	1.3	25.0	0.4	11.1
Isopoda	1.2	33.3	1.0	35.3	7.4	75.0	5.0	50.0	3.3	50.0	4.2	33.3
Brachyura (zoaea)	—	—	—	—	0.1	12.5	—	—	—	—	—	—
Tanaidacea	—	—	—	—	—	—	0.1	16.7	0.1	8.3	—	—
Macrura	—	—	—	—	—	—	0.1	16.7	0.2	16.7	—	—
Mysidacea	—	—	—	—	—	—	0.2	16.7	—	—	0.1	2.8
Insecta	—	—	—	—	0.2	12.5	—	—	—	—	0.1	2.8
Mollusca	—	—	—	—	—	—	—	—	0.1	8.3	4.1	22.2
Echinodermata	—	—	—	—	—	—	—	—	—	—	0.1	2.8
Unidentifiable fragments	2.6	44.4	3.0	52.9	0.1	12.5	0.8	50.0	12.2	66.7	5.4	52.8
No. of fish examined	9		17		8		6		12		36	
Average no. of points allotted per stomach	18.8		13.4		7.3		20.3		17.2		13.2	

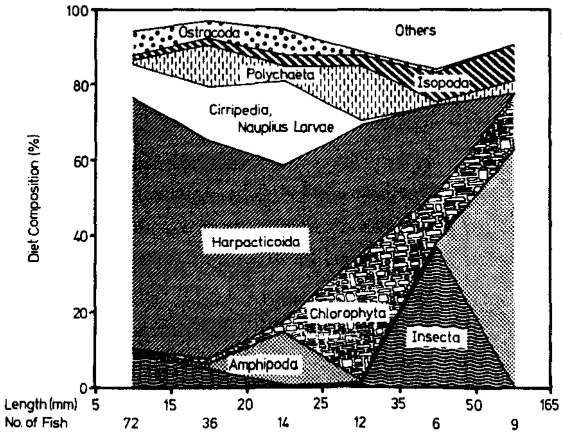

FIGURE 7.—Changes in diet with length of *Diplodus sargus*, collected between August and December 1975, as shown by the comparative feeding index. Food items included in Others are the same as for Figure 8, in addition to the unidentified trochophore larva.

algae, diatoms, chironomid larvae, and hydrozoa as they grow larger.

Identity of Food

Diatoms: two species of the genus *Licmophora*, predominantly *L. pfannkucheae*, as well as *L. ehrenbergii*.

Other algae: the chlorophytan algae of the genus *Ulva* most frequent, although some of the larger size classes also fed on *Caulerpa filiformis* (50-165 mm: 7.5% in summer and 2.9% in winter), *Bryopsis* sp., *Enteromorpha* sp., and *Valonia* sp. Some rhodophytans taken, including *Ceramium* sp., *Hypnea spicivera, Polysiphonia* sp., and *Tayloriella* spp.

Harpacticoid copepods: 12 species, only 4 common, identification was not possible.

Amphipods: 28 species—7 caprellid species including *Caprella danilevskii, C. penantis, C. scaura*, and *Caprellina longicollis*; *Cerapus tubularis; Corophium? acherusicum*, and *C.? triaenonyx*; *Cymadusa* sp.; two *Gammaropsis* species including *G. holmesi*; *Jassa* spp.; *Lysianassa ceratina*; and *L. variegata*; two *Maera* species; *Paramoera capensis*; *Parelasmopus suluensis*; two *Photis* species; *Temnophlias* sp.; *Urothoe* sp.; and three unidentified species.

Isopods: nine species—*Cymodocella pustulata, C. sublevis, Dynamenella huttoni, D. macrocephala, Exosphaeroma antikraussi, Gnathia* sp., *Janiropsis* sp., *Panathura* sp., and a *Stenetrium* species.

Polychaetes: *Dodecaceria pulchra, Eulalia trilineata*, two *Nereis* species, an *Onuphis* sp., and terebellid tentacles most commonly found in the gut contents, as well as *Pista* sp., *Pomatoleois kraussi*, and *Serpula vermicularis*.

Ostracods were not identified.

TABLE 2.—Changes in percentage composition of the food of *Diplodus sargus* with length during the period August to December 1975, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the former, all values greater than 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)											
	5-15		15-20		20-25		25-35		35-50		50-165	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	0.2	4.2	0.6	8.3	2.9	28.6	*33.4*	50.0	13.5	33.3	14.3	55.6
Rhodophyta	—	—	—	—	—	—	0.9	33.3	0.8	33.3	—	—
Chrysophyta	—	—	—	—	—	—	0.7	25.0	8.7	33.3	7.4	11.1
Hydrozoa	—	—	—	—	—	—	—	—	—	—	1.1	11.1
Polychaeta	1.1	20.8	10.4	47.2	4.0	35.7	14.7	33.3	0.9	16.7	4.0	22.2
Crustacea												
Amphipoda	0.3	6.9	1.7	27.8	14.1	57.1	2.4	25.0	6.5	50.0	*62.5*	100.0
Ostracoda	6.0	37.5	5.5	55.6	6.4	64.3	0.8	16.7	0.4	16.7	0.1	11.1
Harpacticoid copepoda	*67.8*	86.1	*58.1*	94.4	*41.6*	100.0	29.6	83.3	17.6	100.0	—	—
Isopoda	1.0	16.7	2.1	25.0	3.4	42.9	3.0	25.0	6.9	50.0	9.8	44.4
Brachyura	0.1	5.6	—	—	0.2	14.3	0.2	8.3	—	—	0.2	11.1
Cirripedia	8.8	36.1	13.9	66.7	21.5	42.9	1.3	8.3	—	—	—	—
Leptostraca	—	—	0.3	5.6	—	—	—	—	—	—	—	—
Tanaidacea	—	—	—	—	0.2	14.3	—	—	—	—	—	—
Macrura	—	—	—	—	0.7	7.1	—	—	—	—	—	—
Insecta	8.8	36.1	4.8	27.8	0.5	21.4	3.8	33.3	*37.2*	50.0	—	—
Mollusca	—	—	—	—	—	—	—	—	—	—	0.3	11.1
Trochophore larvae	4.6	30.6	0.3	5.6	1.6	14.3	1.2	8.3	—	—	—	—
Unidentifiable fragments	1.3	20.8	2.3	30.6	2.9	28.6	8.1	41.7	7.5	50.0	0.2	11.1
No. of fish examined	72		36		14		12		6		9	
Average no. of points allotted per stomach	13.7		17.5		20.4		12.0		14.8		18.2	

Insects: only the larva of the chironomid *Telmatogeton minor*.

Brachyurans: *Rhyncoplax bovis* and the gut of an unidentified crab (in a single case).

Molluscs: *Gibbula rosea, Helcion pruinosus, Philine aperta*, and a rhaciglossid (no shell, so not possible to identify further).

Hydrozoans: *Symplectoscyphus* sp. and *Thecocarpus formosus* were ingested by one fish in the 50- to 70-mm size class.

Echinoderms: *Parechinus* sp.

Tanaidaceans: *Leptochelia barnardi* most commonly found, also an *Apseudes* sp.

Mysidaceans: only one species, *Mysidops similis*, could be identified with any certainty.

Diplodus cervinus

The diet of *Diplodus cervinus* is illustrated in Figure 8 and Table 3 ($n = 67$). The juveniles (10-20 mm) fed mainly on harpacticoid copepods and chironomid larvae. In the next size class (20-35 mm), juveniles of the sand shrimp, *Palaemon pacificus*, were taken instead of chironomid larvae. This trend continues in the 35- to 50-mm size class, the diet being composed largely of *P. pacificus* as well as harpacticoid copepods. Polychaetes are more important in this size group, a trend which is maintained in all larger size classes. In the larger fish, there was again a changeover, the percentage of amphipods taken being 65.7% (50-75 mm) and 27.6% (75-100 mm). Unidentifiable crustacean fragments in these size classes composed 12.6% and 47.9%, respectively, which is partly explained by the fact that 6 of the 40 fish were taken at night and their stomach contents were largely digested and thus indistinguishable. The diet of the largest size class (100-135 mm) was made up mainly of polychaetes.

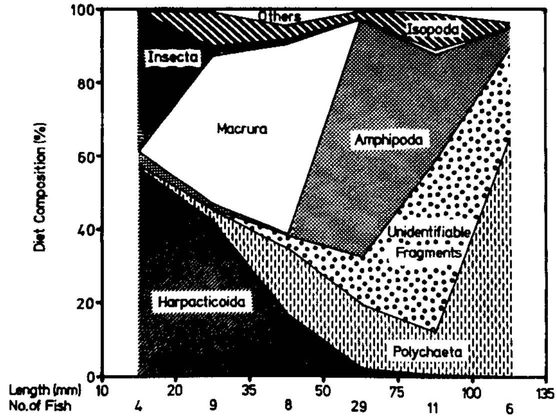

FIGURE 8.—Changes in diet with length in *Diplodus cervinus*, as shown by the comparative feeding index. Food items included in Others are: chlorophytan algae, cirripede nauplii, coralline algae, molluscs, mysidaceans, ostracods, tanaidaceans, and the unidentified trochophore larva.

Identity of Food

The diet was composed of almost all the food species listed for *D. sargus*, although in differing proportions, as well as the following: *Cymodocella eutylos* (isopod), *Littorina knysnaensis* (mollusc),

TABLE 3.—Changes in the percentage composition of the food of *Diplodus cervinus* with length, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the latter, all values exceeding 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)											
	10-20		20-35		35-50		50-75		75-100		100-135	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	—	—	—	—	4.6	12.5	—	—	—	—	—	—
Rhodophyta	—	—	—	—	—	—	—	—	—	—	1.9	16.7
Polychaeta	0.2	25.0	3.8	33.3	17.6	50.0	17.2	72.4	11.4	18.0	*65.4*	82.3
Crustacea												
Amphipoda	4.1	25.0	1.0	33.3	0.4	25.0	*65.7*	74.9	27.6	45.0	5.8	33.3
Ostracoda	—	—	0.2	22.2	—	—	—	—	0.6	9.0	—	—
Harpacticoid copepoda	*56.5*	100.0	*41.6*	77.8	16.5	87.5	2.2	51.7	0.1	9.0	—	—
Isopoda	—	—	10.0	44.4	4.2	25.0	1.5	20.7	11.0	27.0	1.7	16.7
Cirripedia (nauplii)	—	—	—	—	—	—	0.5	6.9	—	—	—	—
Macrura	—	—	*41.2*	44.4	*53.2*	50.0	—	—	1.0	9.0	—	—
Tanaidacea	—	—	—	—	—	—	0.2	6.8	—	—	—	—
Mysidacea	—	—	—	—	—	—	0.1	3.4	—	—	—	—
Insecta	*39.0*	50.0	2.2	55.6	0.4	12.5	—	—	—	—	—	—
Mollusca	—	—	—	—	—	—	—	—	0.4	9.0	1.9	16.7
Trochophore larvae	0.2	25.0	—	—	—	—	—	—	—	—	—	—
Unidentifiable fragments	—	—	—	—	3.1	50.0	12.6	79.3	*47.9*	36.0	23.3	33.3
No. of fish examined	4		9		8		29		11		6	
Average no. of points allotted per stomach	8.3		19.3		8.0		10.0		6.4		11.1	

Phoxostoma sp. (amphipod), and *Corallina* sp. (rhodophytan alga).

Sarpa salpa

The percentage composition of the diet of *Sarpa salpa* is illustrated in Figure 9 and Table 4. The food habits of this species changed from being primarily a carnivore as a juvenile to a herbivore as a subadult.

Juveniles in the 10- to 25-mm size classes fed mainly on harpacticoid copepods. In the next size class (25-35 mm), however, the total animal contribution is only 15.1%, diatoms and rhodophytan algae being most important. Diatoms are taken in decreasing amounts from then on and those fish >75 mm SL fed predominantly on chlorophytan and rhodophytan algae.

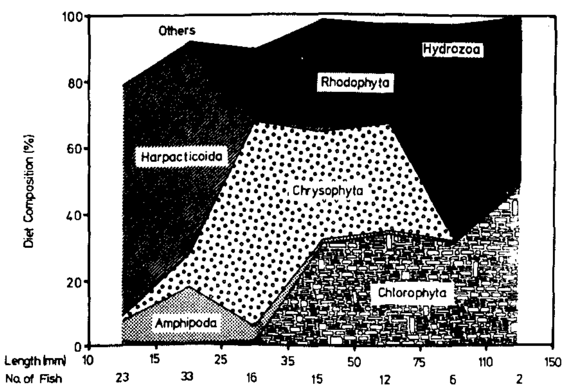

FIGURE 9.—Changes in diet with length of *Sarpa salpa*, as shown by the comparative feeding index. Food items included in Others are: bryozoans, cirripede nauplii, crab zoaea, fish muscle, insects, isopods, leptostracans, mysidaceans, ostracods, polychaetes, rhaciglossid molluscs, and tanaidaceans.

Identity of Food

Chlorophytan algae: eight species—*Bryopsis* sp., *Caulerpa filiformis*, *Chaemaedoris delphini*, *Cladophora* spp.,*Enteromorpha* sp.,*Rhizoclonium* sp., and *Ulva* sp.

Rhodophytan algae: *Ceramium* sp., *Champia compressa*, *Hypnea spicifera*, *Polysiphonia* sp., and *Tayloriella* sp. commonly taken as well as *Acrosorium* sp., *Arthrocardia* sp., *Centroceras* sp., *Corallina* spp., *Polyzonia elegans*, and *Pterosiphonia cloiophylla*.

Chrysophytan algae: three species of diatoms—*Isthmia enervis*, *Licmophora ehrenbergii*, and *L. pfannkucheae*.

Hydrozoans: *Gattya humilis* commonly ingested by the 75- to 100-mm size class, whereas *Sertularella* sp. and *Thecocarpus formosus* were uncommon.

Polychaetes: only two species of *Nereis*.

Isopods: uncommon, but six species were found—*Dynamenella huttoni*, *D. macrocephala*, *Gnathia* sp., *Janiropsis* sp., *Panathura* sp., and *Stenetrium* sp.

TABLE 4.—Changes in the percentage composition of the food of *Sarpa salpa* with length, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the latter, all values exceeding 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)													
	10-15		15-25		25-35		35-50		50-75		75-100		125-150	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	0.3	8.7	—	—	0.9	31.3	*31.2*	92.0	*34.0*	91.7	*30.6*	100.0	*48.3*	100.0
Rhodophyta	—	—	0.4	9.1	21.3	62.5	*32.3*	76.0	28.6	66.7	*45.9*	83.3	*50.1*	100.0
Chrysophyta	0.2	8.7	9.3	24.2	*62.7*	100.0	*32.4*	68.0	*33.4*	66.7	—	—	—	—
Hydrozoa	—	—	—	—	—	—	—	—	0.1	16.7	20.5	50.0	0.8	50.0
Polychaeta	5.1	17.4	2.6	30.3	—	—	—	—	0.4	8.3	0.1	16.7	—	—
Crustacea														
Isopoda	1.7	17.4	0.9	30.3	0.1	6.3	—	—	—	—	—	—	—	—
Amphipoda	7.3	30.4	17.8	63.6	4.2	50.0	0.9	16.0	0.1	16.7	0.3	33.3	0.8	50.0
Ostracoda	6.7	26.1	1.4	36.4	0.1	6.3	0.1	12.0	—	—	—	—	—	—
Harpacticoid copepoda	*71.0*	87.0	*64.5*	72.7	0.5	18.8	1.4	24.0	—	—	—	—	—	—
Cirripedia (nauplii)	5.5	22.0	2.1	18.2	—	—	—	—	—	—	—	—	—	—
Brachyura (zoaea)	—	—	0.1	3.0	0.1	12.5	—	—	—	—	—	—	—	—
Leptostraca	0.1	4.4	—	—	—	—	—	—	—	—	—	—	—	—
Insecta	0.1	4.4	0.2	3.0	0.1	12.5	—	—	—	—	—	—	—	—
Bryozoa	—	—	—	—	—	—	—	—	—	—	0.1	16.7	—	—
Mollusca	—	—	—	—	—	—	—	—	—	—	0.1	16.7	—	—
Pisces	—	—	—	—	0.2	6.3	—	—	—	—	—	—	—	—
Unidentified fragments and sand	2.0	26.1	0.7	24.2	9.8	31.3	1.7	32.0	3.4	41.7	2.4	50.0	—	—
No. of fish examined	23		33		16		25		12		6		2	
Average no. of points allotted per stomach	7.8		9.5		13.8		15.7		16.5		15.5		28.0	

Amphipods: also uncommon except in juveniles which took the following 15 species: *Caprella cicur* and two other species of *Caprella*, *Cerapus* sp., *Corophium* sp., *Gammaropsis* sp., *Lysianassa ceratina*, *L. variegata*, *Jassa* sp., *Maera* sp., *Paramoera capensis*, *Parelasmopus suluensis*, *Photis* sp., and two unidentified species.

Harpacticoid copepods: eight species.

Insects: larvae of the chironomid *Telmatogeton minor*.

Tanaidaceans: *Leptochelia barnardi*, uncommon.

Molluscs: rhaciglossid.

DENTITION AND GUT MORPHOLOGY

Diplodus cervinus—there are six upper and four lower incisors which are narrower than those of *D. sargus*, and there are fewer molars, the number increasing with age (Figure 10A). This would indicate that adult *D. cervinus* feed on softer foods than *D. sargus*, which is borne out as the diet of the former consists primarily of polychaetes, whereas the latter took amphipods and molluscs as well. The gut of *D. cervinus* is short with a G/S ratio of 0.7 in a 16.5-mm fish and 0.95 in one 74 mm long.

Diplodus sargus—there are four stout incisors and three to four rows of fairly large molars in each jaw (Figure 10B), the latter increasing in size and number with age. The teeth are those of a typical omnivore (Weatherly 1972). The G/S ratio was 0.76 in a 16.5-mm fish and this is within the range of omnivores as defined by Nikolsky (1963).

Sarpa salpa—this species shows a change in dentition correlated with age and diet. The young fish are carnivorous and have short, pointed coni-

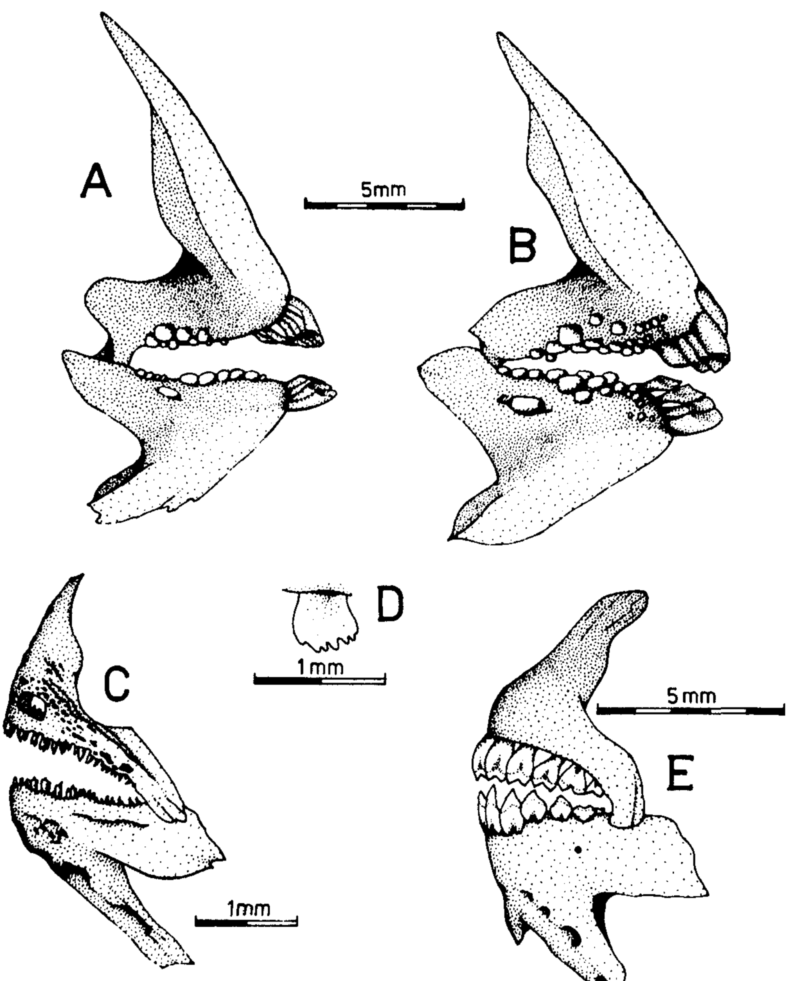

FIGURE 10.—Dentition. A. Medial view of the left upper and lower jaws of *Diplodus cervinus* (MSC 75-36, 94 mm SL). B. Medial view of the left upper and lower jaws of *D. sargus* (MSC 75-34, 107 mm SL). C. Lateral view of the upper and lower jaws of a juvenile *Sarpa salpa* (MSC 75-39, 20 mm SL). D. Lateral view of a single tooth of a subadult *S. salpa* (MSC 75-37, 39 mm SL). E. Lateral view of the upper and lower jaws of an adult *S. salpa* (RUSI 74-323, 99 mm SL).

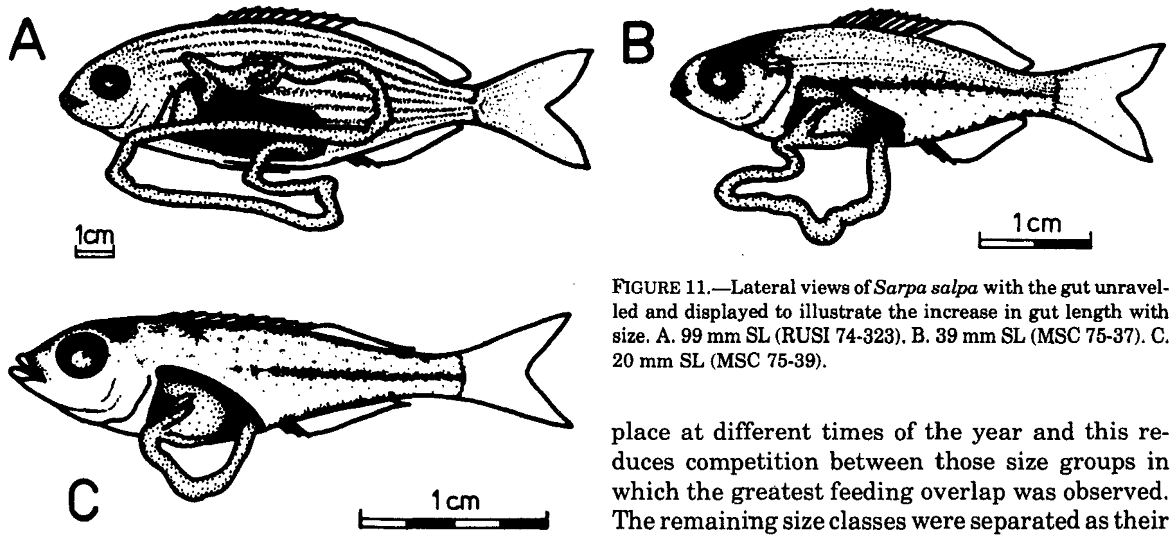

FIGURE 11.—Lateral views of *Sarpa salpa* with the gut unravelled and displayed to illustrate the increase in gut length with size. A. 99 mm SL (RUSI 74-323). B. 39 mm SL (MSC 75-37). C. 20 mm SL (MSC 75-39).

cal teeth to grasp prey (Figure 10C). Multicusped, incisiform teeth begin to break through when the fish are about 20 mm long (Figure 10D). The pointed teeth are completely replaced by the time the fish are 35 mm long, after which they feed predominantly on algae (approximately 60% CFI). The multiple cusps wear away and the teeth are bicuspid incisiform by the time the fish are 65 to 75 mm long (Figure 10E). These can nip at algae and the diet is composed of 65 to 77% plant matter at this stage.

The gut shows a corresponding change in length with diet, a long gut being characteristic of a herbivore. The G/S ratio increases from 0.86 in a 20-mm fish (Figure 11C, typically omnivorous) to 1.36 in a 39-mm fish (Figure 11B), and 2.66 in a 99-mm individual (Figure 11A). This latter value is typical of a herbivore (Nikolsky 1963), although not as pronounced as in some other herbivorous fish species.

DISCUSSION

A number of fish species occur as juveniles or spend their entire life cycle in the eastern Cape intertidal (see description under Study Area). The family Sparidae includes the largest number and the present investigation of the trophic relationships of three of these was initiated as competitive interaction is often most vigorous in closely related fish (Fryer and Iles 1972). There is an intense dietary overlap in some cases and the available resources are subdivided in two main ways. Recruitment of juveniles of the three species takes place at different times of the year and this reduces competition between those size groups in which the greatest feeding overlap was observed. The remaining size classes were separated as their diets were different.

Small juveniles of the three species have the most similar diets of all size classes studied. The resulting competition is reduced by two mechanisms. Firstly, juveniles of *Sarpa salpa* occur in the tide pools primarily from July to September (Figure 5) whereas those of *Diplodus cervinus* were found during October and November (Figure 4) and *D. sargus* was present throughout the year (Figure 3). Secondly, at the time of maximal competition (July-November), the diet of small *D. sargus* includes food items not taken at other times of the year, e.g., chironomid larvae and cirripede nauplii (Figure 7). This may be due to either the presence of these prey items only at that time of the year and/or to the effects of competition forcing *D. sargus* to include them in its diet. A combination of both factors would appear to be operative in the case of the chironomids as the larvae were obtained in bottom samples taken in October-November and not in March. No data are available for cirripede nauplii, crab zoaea, and the unidentified trochophore larva as plankton samples were not taken.

Competition for food is greatly reduced by the time the three sparids are about 25 to 30 mm long. At this stage, *S. salpa* feeds mainly on diatoms and red algae (Figure 9); *D. cervinus* ingests *Palaemon pacificus*, harpacticoid copepods, and isopods (Figure 8); and *D. sargus* takes green algae, harpacticoids, chironomid larvae, and cirripede nauplii (Figures 6, 7). The separation is equally distinct in subadult fish as *S. salpa* is then a herbivore, *D. cervinus* takes polychaetes, some amphipods, and isopods, while *D. sargus* feeds on amphipods and green algae. The overlap on amphipods by the latter two species may be partially compensated for by behavioral separation. *Diplodus cervinus* is a secretive substrate feeder whereas *D. sargus* is a more open water fish tending to feed on vertical rock surfaces away from the bottom. The fact that neither species was very common intertidally in these size classes may also contribute towards a reduction in competition.

The diet of large juvenile *S. salpa* is unusual in that it consists mainly of diatoms and epiphytic rhodophytan algae which occur commonly on corallines, *Hypnea spicifera* and *Tayloriella* spp. (M. H. Giffen, pers. commun.). The fish must, therefore, selectively separate these food items as few fragments of the algae on which they grow were found in the stomach contents. This is in contrast to *Rhabdosargus holubi*, also a sparid, which ingests algae for their epiphytic diatoms rather than separating them, even though the algae are not digested (Blaber 1974). The situation may be similar to this in larger *S. salpa* as the rectal contents appeared to be relatively undigested and fewer diatoms were observed on the algae (Figure 12).

Temporal separation of juveniles to reduce competition has not been reported previously for tide pool fish species as far as I am aware, although it has been observed in two pelagic plankton feeders from the Adriatic, the anchovy and sardine (Vučetič 1975). Large dietary overlaps have been noted in several intertidal fish, including blennies, clinids, gobies, and labrids (Gibson 1968, 1972). These fed predominantly on crustaceans and it is possible that similar mechanisms reduce competitive pressure amongst them, although this was not determined as samples were only taken for 2 mo.

The data presented indicates that *D. cervinus* is a carnivore, *D. sargus* is an omnivore, and *S. salpa* an omnivore when juvenile and a herbivore when adult. Similar feeding habits were found for adults of the same three species in the Klein River estuary (Talbot 1954). The dentition and gross gut morphology changed with size and this was most marked in *S. salpa*, corresponding with the observed diet. Comparable transformations have been reported for other fish species (Nikolsky 1963).

Two other sparids, *Sparodon durbanensis* and *R. holubi*, cohabit with those studied in the littoral zone. The few specimens examined had fed mainly on harpacticoid copepods as small juveniles, with a resultant overlap with *D. sargus* as all three occurred in the research area in November-December. Large specimens were not examined, but *R. holubi* appears to be an omnivore as a juvenile in estuaries and a carnivore feeding on molluscs as an adult (Talbot 1954; Blaber 1974). Adult *S. durbanensis* are carnivores feeding on small fish, molluscs, and crustaceans (Biden

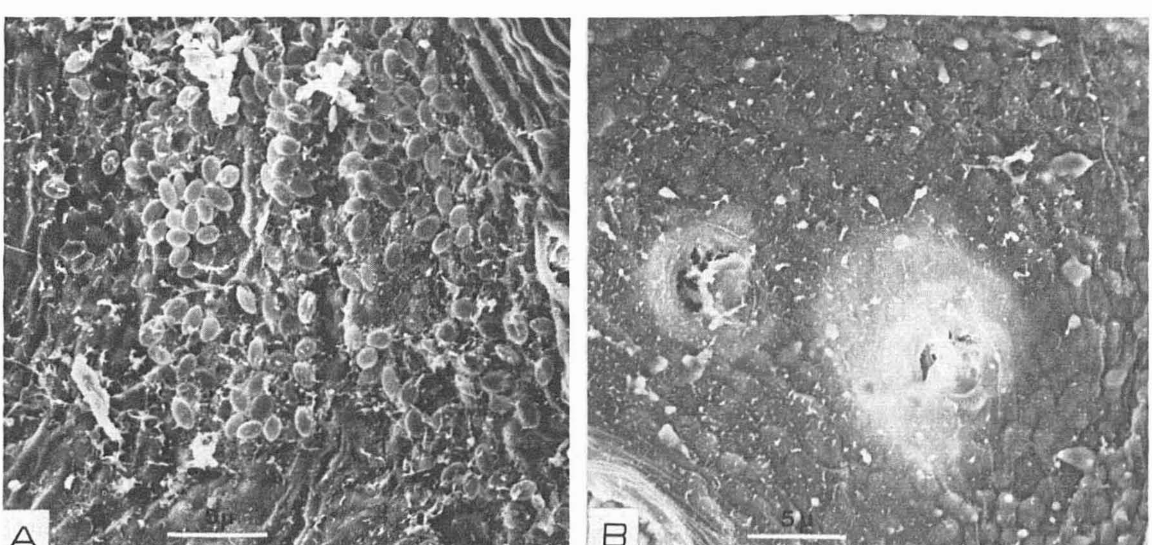

FIGURE 12.—Scanning electron micrograph of the surface of a chlorophytan alga, *Ulva* sp., removed from the gut of *Sarpa salpa* (147 mm SL) to show the disappearance of diatoms. A. Oesophageal sample. B. Rectal sample.

1954). Competitive pressure is, therefore, minimized between the five sparid fish species commonly occurring in the littoral zone.

ACKNOWLEDGMENTS

This study was submitted in partial fulfillment of the requirements for an M.S. degree in the J. L. B. Smith Institute of Ichthyology, Rhodes University, Grahamstown. I thank G. S. Butler, B. J. Hill, P. B. N. Jackson, M. van Harten, and R. Winterbottom for assistance in the field and/or valuable criticisms. I am also grateful to the following, who identified many of the food items: C. Griffiths (amphipods) and B. F. Kensley (isopods and brachyurans), University of Cape Town; M. H. Giffen (diatoms), Fort Hare University, Alice; and S. C. Seagrief (algae), Rhodes University, Grahamstown. R. Winterbottom provided useful suggestions and criticisms as my supervisor, and carefully reviewed and commented on the manuscript, as did R. N. Gibson, Dunstaffnage Marine Research Laboratory, Argyll, Scotland, and E. S. Hobson, National Marine Fisheries Service, NOAA, Tiburon, Calif. Their assistance was greatly appreciated as was that of J. Pote who typed the manuscript. Finally, I thank the following for financial assistance: J. L. B. Smith Institute of Ichthyology (Hugh Le May scholarship), CSIR (research bursary), and Rhodes University (Research Council Grant No. 2857, R. Winterbottom principal investigator).

LITERATURE CITED

BARNARD, K. H.
1927. A monograph of the marine fishes of South Africa. Ann. S. Afr. Mus. 21(2):419-1065.

BIDEN, C. L.
1954. Sea-angling fishes of the Cape: a natural history of some of the principal fishes caught by sea anglers and professional fishermen in Cape waters. 2d ed. Juta and Co. Ltd., Capetown and Johannesb., 304 p.

BLABER, S. J. M.
1974. Field studies of the diet of *Rhabdosargus holubi* (Pisces: Teleostei: Sparidae). J. Zool. (Lond.) 173:407-417.

FROST, W. E.
1943. The natural history of the minnow, *Phoxinus phoxinus*. J. Anim. Ecol. 12:139-162.

FRYER, G., AND T. D. ILES.
1972. The cichlid fishes of the great lakes of Africa: their biology and evolution. Oliver & Boyd, Edinb., 641 p.

GANNON, J. E.
1976. The effects of differential digestion rates of zooplankton by alewife, *Alosa pseudoharengus*, on determinations of selective feeding. Trans. Am. Fish. Soc. 105:89-95.

GIBSON, R. N.
1968. The food and feeding relationships of littoral fish in the Banyuls region. Vie Milieu, Sér. A, 19:447-456.
1972. The vertical distribution and feeding relationships of intertidal fish on the Atlantic coast of France. J. Anim. Ecol. 41:189-207.

HOBSON, E. S.
1974. Feeding relationships of teleostean fishes on coral reefs on Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.

HOBSON, E. S., AND J. R. CHESS.
1973. Feeding oriented movements of the atherinid fish *Pranesus pinguis* at Majuro Atoll, Marshall Islands. Fish. Bull., U.S. 71:777-786.

HYNES, H. B. N.
1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J. Anim. Ecol. 19:36-58.

KIONKA, B. C., AND J. T. WINDELL.
1972. Differential movement of digestible and indigestible food fractions in rainbow trout, *Salmo gairdneri*. Trans. Am. Fish. Soc. 101:112-115.

NIKOLSKY, G. V.
1963. The ecology of fishes. Academic Press, N.Y., 352 p.

PINKAS, L.
1966. A management study of the California barracuda *Sphyraena argentea* Girard. Calif. Dep. Fish Game, Fish. Bull. 134, 58 p.

RANDALL, J. E.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665-847.

ROUND, F. E.
1971. Benthic marine diatoms. Oceanogr. Mar. Biol. Annu. Rev. 9:83-139.

ROYCE, W. F.
1972. Introduction to the fishery sciences. Academic Press, N.Y., 351 p.

SMITH, J. L. B.
1965. The sea fishes of southern Africa. Cape and Transvaal Printers Ltd., Cape Town, 580 p.

SWYNNERTON, G. H., AND E. B. WORTHINGTON.
1940. Note on the food of fish in Haweswater (Westmorland). J. Anim. Ecol. 9:183-187.

TALBOT, F. H.
1955. Notes on the biology of the white stumpnose, *Rhabdosargus globiceps* (Cuvier), and on the fish fauna of the Klein river estuary. Trans. R. Soc. S. Afr. 34:387-407.

TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596), 17 p.

VUČETIĆ, T.
1973. Synchronism of the spawning season of some pelagic fishes (sardine, anchovy) and the timing of the maximal food (zooplankton) production in the Central Adriatic. Pubbl. Staz. Zool. Napoli, 39 Suppl. 1:347-365.

WEATHERLY, A. H.
1972. Growth and ecology of fish populations. Academic Press, Lond., 293 p.

WINDELL, J. T.
1971. Food analysis and rate of digestion. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 215-226. Blackwell Scientific Publications, Oxf. and Edinb.