

Diets of *Diplodus sargus capensis* and *D. cervinus hottentotus* (Pisces: Sparidae) on the Tsitsikamma coast, South Africa

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Diets of *Diplodus sargus capensis* and *D. cervinus hottentotus*, sampled on the Tsitsikamma coast, are described. *D. sargus* was a generalist, feeding on a wide variety of reef associated invertebrates and algae. *D. cervinus* was more of a specialist feeding on comparatively few prey groups, the most important being polychaetes and amphipods. Juveniles of both species showed considerable spatial and dietary overlap, feeding predominantly on amphipods, polychaetes and harpacticoid copepods. Larger fish showed an increase in the range of prey species taken and dietary overlap was diminished. The dietary differences between these two species are thought to contribute to greater abundance and habitat range in *D. sargus*.

Key words: Reef fish, diet, habitat preference, marine reserve.

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Introduction

The blacktail, *Diplodus sargus capensis* (Smith 1844), is found from Angola to Mozambique and off southern Madagascar (Smith & Heemstra 1986). It is a common species inhabiting the lower reaches of estuaries (Day *et al.* 1981), tide pools (Beckley 1985), sandy beach surf zones (Lasiak 1986; Bennett 1989) and shallow inshore reefs (Beckley & Buxton 1989; Burger 1991). The zebra, *D. cervinus hottentotus* (Smith 1844), has a more restricted distribution from Cape Point to Sodwana Bay (Smith & Heemstra 1986). It is less abundant than blacktail, and although recorded in all of the above habitats, is most common on inshore reefs down to about 25 m (Buxton & Smale 1984; Burger 1991). Both species are important to the recreational rock-and-surf fishery (Van der Elst & Adkin 1991).

Although a considerable amount has been published on the diet of *D. sargus*, most of this has focused on the diet of juveniles in the south-eastern Cape. These studies have shown that juvenile *D. sargus* feed predominantly on small crustaceans and chlorophytes

in a variety of nursery habitats, including intertidal rock pools (Christensen 1978), estuaries (Whitfield 1985) and the surf zone habitat (Lasiak 1986). The diet of larger *D. sargus* in Natal (Joubert & Hanekom 1980) and off St Croix Island in Algoa Bay (Coetzee 1986) indicated that they were omnivorous, ingesting a wide variety of invertebrates and algae. *D. cervinus* has received little attention except for a study by Christensen (1978) who showed that juveniles from rock pools in the eastern Cape were carnivorous, feeding on small crustaceans, chironomid larvae and polychaetes.

As part of an ongoing investigation into the biology of reef fishes in the Tsitsikamma National Park, the objectives of this study were to describe and compare diets, to investigate seasonal and size related differences in diet and to examine how diet relates to habitat preference and distribution of the two species. This work also formed part of a larger study on the biology, distribution and abundance of both *Diplodus* species in the Tsitsikamma National Park (Mann 1992).

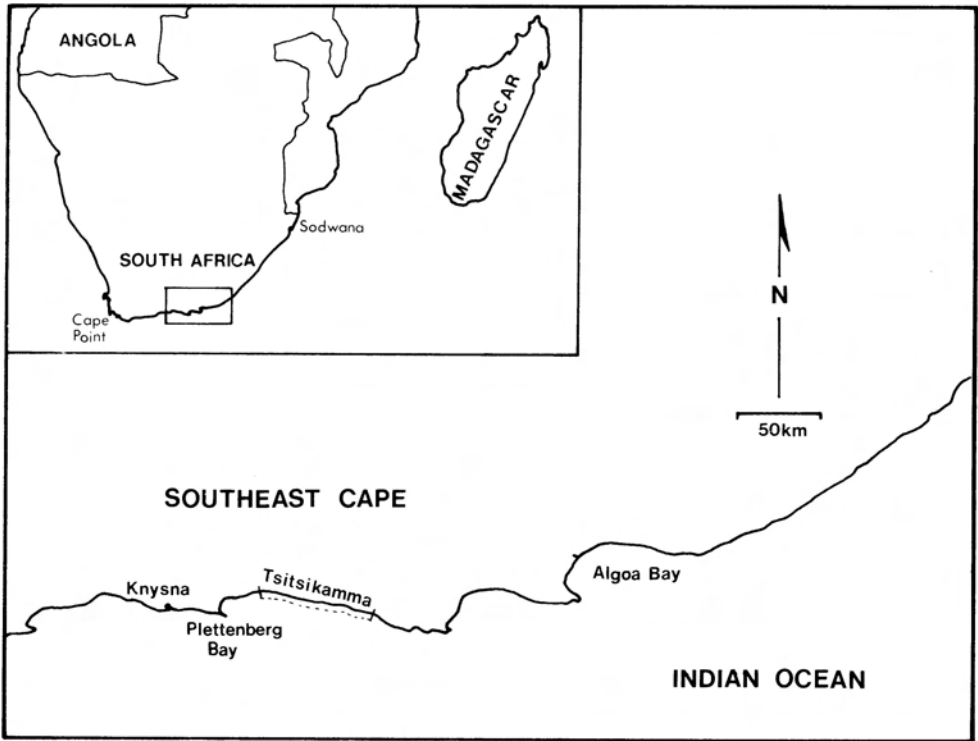


Fig. 1. Map of the study area showing places mentioned in the text.

Methods

Most of the data were collected in the Tsitsikamma National Park (TNP), a large marine reserve situated on the south-eastern coast of South Africa (Fig. 1), between Oubosstrand and Nature's Valley. The reserve covers 65.7 km of coastline and extends 5.6 km offshore except for a short section on the western boundary which extends 0.8 km offshore (Hockey & Buxton 1989). It has been closed to fishing for 26 years (except for a 3 km section of coast adjacent to Storms River where shore angling is permitted), and for this reason is considered pristine (Buxton & Smale 1989). Additional samples were collected at two local spearfishing competitions, one at Knysna (8 October 1989) and the other at Plettenberg Bay (18 August 1990).

Fish were sampled by spear and line from numerous areas within the TNP and off Sout River just outside the western boundary of the park. Juveniles (< 100 mm FL) were collected from tidal rock pools and subtidal gullies using rotenone ichthyocide. Total and gutted mass (grammes) and the fork length (millimetres) were measured for each fish sampled. Stomachs, removed by severing the oesophagus near to the buccal cavity and the intestine just anterior to the pyloric caecae, were preserved in a buffered 10 percent formalin solution. To study changes in seasonal feeding intensity, stomach contents were

weighed and an index of stomach fullness (SFI) was calculated (Hyslop 1980):

$$SFI = \frac{\text{Stomach contents (g)} \times 100}{\text{Gutted fish (g)}}$$

Stomach contents were identified to the lowest possible taxon and expressed in terms of frequency of occurrence and volume (Buxton & Clarke 1991). In smaller fish bulk contribution was determined using a visual percentage volume estimate (Christensen 1978), whereas in larger fish, bulk was determined from wet mass of prey. Finally a ranking index (RI), the frequency of occurrence multiplied by the mean percentage volume/ weight (Hobson 1974) was computed for each prey group.

Seasonal changes in feeding were investigated by comparing diets of fish caught during summer (October to March) with those caught during winter (April to September).

To assess changes in diet with size fish were divided into three size classes according to states of maturity: juveniles (32-150 mm FL), sub-adults (151 - 225 mm FL for *D. sargus*, 151 - 300 mm FL for *D. cervinus*) and adults (*D. sargus* > 225 mm FL and *D. cervinus* > 300 mm FL). Overlap between the two species was calculated using the Spearman rank correlation coefficient (r_s) (Fritz 1974).

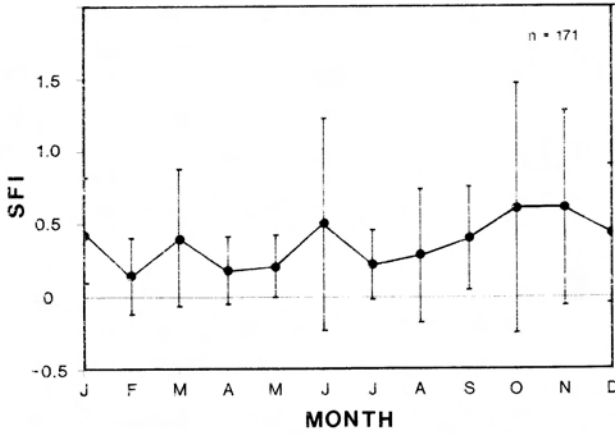


Fig. 2. Mean monthly stomach fullness indices for *Diplodus sargus capensis*, sampled in the Tsitsikamma National Park from April 1989 to December 1990.

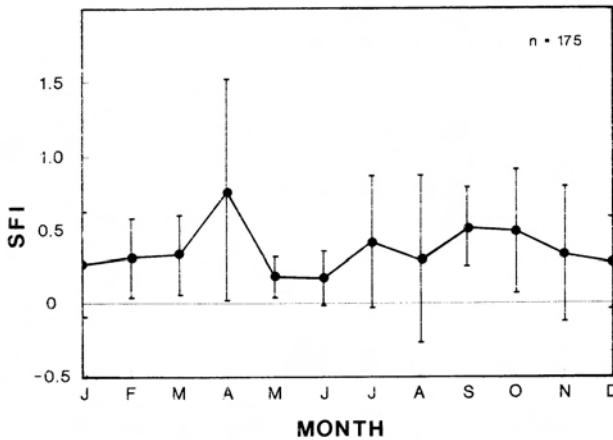


Fig. 3. Mean monthly stomach fullness indices for *Diplodus cervinus hottentotus*, samples in the Tsitsikamma National Park from April 1989 to December 1990.

Results

A total of 203 *D. sargus* and 189 *D. cervinus* were sampled between May 1989 to December 1990 of which 68,5% and 80% contained food, respectively. Calculation of a monthly stomach fullness index (SFI) showed little seasonal variation in the amount of food consumed by both species (Figures 2 & 3). *D. sargus* did, however, show a higher mean SFI = 0,435 for the summer months (October to March) as opposed to the winter mean of 0,298.

Diet of *D. sargus*

A total of 34 juvenile *D. sargus* (41–150 mm FL) were collected from intertidal rockpools and subtidal gullies. These fish were often found in large shoals where they appeared to feed on vertical surfaces of the substratum or in midwater away from cover. Amphipods, polychaetes, copepods and echinoids were the most important dietary components (Table 1), gammarid and caprellid amphipods ranking as the most important prey items both in terms of frequency of occur-

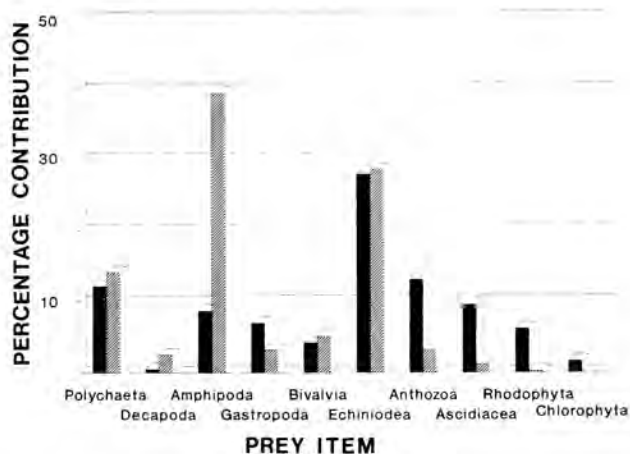


Fig. 4. Percentage contribution to the diet of prey consumed by *Diplodus sargus capensis* in the Tsitsikamma National Park in summer (solid) and winter (hatched), $n=139$.

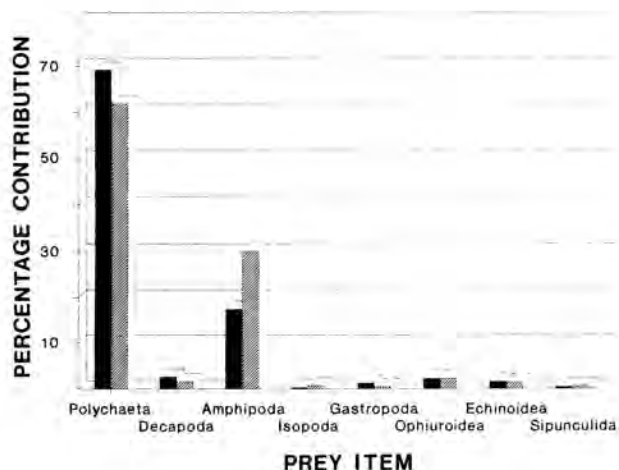


Fig. 5. Percentage contribution to the diet of prey consumed by *Diplodus cervinus hottentotus* in the Tsitsikamma National Park in summer (solid) and winter (hatched), $n=150$.

rence (73,5%) and percentage volume (49,7%). Harpacticoid copepods appeared to be an important food source to only the very small juveniles (41 – 60 mm FL), amphipods and small polychaete worms becoming more important in the larger juveniles (50 – 150 mm FL). The occurrence of sea urchin tube feet in the stomachs showed evidence of a browsing habit, similar to that of juvenile *Sparodon durbanensis* (Buxton & Clarke

1991). In contrast to the findings of others (Christensen 1978, Whitfield 1985, Lasiak 1986), juvenile *D. sargus* in the TNP consumed very little algae.

Sub-adult *D. sargus* (151–225mm FL) were found in shallow subtidal areas where they occurred in loose shoals of similarly sized individuals. They fed on a wide range of prey organisms associated with a rocky substra-

Table 1

Stomach content analysis of juvenile *Diplodus sargus capensis* between 41 mm and 150 mm fork length, sampled in rock pools and in shallow sub-tidal waters in the TNP from April 1989 to December 1990 (n=34)

Prey Species	% Freq. Occ.	Mean % Vol.	Rank
Amphipoda	73,52	49,69	36,53
Caprellidea	38,23		
Gammaridea	55,88		
Polychaeta	23,52	8,05	1,89
Copepoda	8,82	7,20	0,63
Harpacticoidea	8,82		
Echinoidea	8,82	5,44	0,48
<i>Parechinus angulosus</i>	8,82		
Pisces	11,76	3,44	0,40
Scales	11,76		
Anthozoa	14,70	2,64	0,38
Insecta	14,70	2,50	0,36
<i>Telmatogeton minor</i>	14,70		
Isopoda	14,70	2,26	0,33
Gastropoda	11,76	2,79	0,32
Bivalvia	5,88	3,82	0,22
Chlorophyta	2,94	2,44	0,07
Ascidiacea	2,94	2,05	0,06
Decapoda	2,94	0,44	0,01
Mysidacea	2,94	0,29	T
Rhodophyta	2,94	0,23	T
Cirripedia	2,94	0,14	T
Tanaidacea	5,88	0,04	T
<i>Apseudes digitalis</i>	5,88		
Unidentified	14,70	6,47	0,95

Trace (T) = Items with a rank of less than 0,01

tum. Echinoids, polychaetes, anthozoans, gastropods and bivalves were among the most important prey components (Table 2). Relative to the juveniles, amphipods were less important in the diet, sub-adult fishes showing a preference for slightly larger prey items. The diversity of prey consumed by *D. sargus* is characteristic of the feeding behaviour of searchers (Hughes 1980).

Adult *D. sargus* (226–331 mm FL) were also found to occur in aggregations of similarly sized individuals predominantly in the in-shore surf zone and seldom deeper than 15 metres. Little change was evident in the diet of sub-adult and adult fish, except for an increase in the relative amount of red bait, (*Pyura stolonifera*) (Table 3). Although rhodophytes were consumed fairly frequently (28,8% occurrence) they only consti-

Table 2

Stomach content analysis of sub-adult *Diplodus sargus capensis* between 151 mm and 225 mm fork length, sampled in the TNP from April 1989 to December 1990 (n=53)

Prey Species	% Freq. Occ.	Mean % Mass	Rank
Echinoidea	47,16	22,97	10,83
<i>Parechinus angulosus</i>	47,16		
Polychaeta	35,84	10,52	3,77
<i>Lysidice natalensis</i>	3,70		
<i>Lepidonotus semitectus</i>	3,70		
<i>Serpula vermicularis</i>	3,70		
Anthozoa	33,96	8,96	3,04
<i>Bunodactis reynaudi</i>	9,25		
Gastropoda	28,30	9,50	2,69
<i>Patella</i> spp.	11,11		
<i>Fissurella mutabilis</i>	3,70		
<i>Amblychilepas scutellum</i>	3,70		
<i>Littorina</i> spp.	3,70		
Bivalvia	28,30	8,52	2,41
<i>Perna perna</i>	7,40		
<i>Septifer bilocularis</i>	3,70		
Amphipoda	26,41	5,84	1,54
Gammaridea	18,51		
Caprellidea	7,40		
Ascidiacea	16,98	7,81	1,32
<i>Pyura stolonifera</i>	5,55		
Rhodophyta	22,64	4,30	0,97
<i>Duthiophycus setchelli</i>	9,25		
Decapoda	16,98	4,49	0,76
<i>Cyclograpsus punctatus</i>	1,85		
<i>Plagusia chabrus</i>	1,85		
Ophiuroidea	11,32	2,79	0,31
Holothuridae	9,43	2,94	0,27
Porifera	11,32	1,83	0,20
Bryozoa	13,20	0,78	0,10
Sipunculida	5,66	1,32	0,07
<i>Phascolosoma</i> spp.	5,66		
Pisces	3,77	1,96	0,07
Cirripedia	11,32	0,64	0,07
Polyplacophora	5,66	0,98	0,05
Isopoda	3,77	0,41	0,01
<i>Dynamenella huttoni</i>	1,85		
Asteroidea	1,88	0,56	0,01
Hydrozoa	7,54	0,11	T
Cephalopoda	1,88	0,37	T
Pycnogonida	3,77	0,13	T
Insecta	1,88	0,20	T
Chlorophyta	1,88	0,18	T
Tanaidacea	1,88	0,18	T
Unidentified	9,43	1,60	0,15

Trace (T) = Items with a rank of less than 0,01

tuted 4,25 percent of the diet by volume. This was different from dietary studies done in Natal (Joubert & Hanekom 1980) and off St Croix Island near Port Elizabeth (Coetzee

Table 3

Stomach content analysis of adult *Diplodus sargus* capensis between 226 mm and 331 mm fork length, sampled in the TNP from April 1989 to December 1990 (n=52)

Prey Species	% Freq. Occ.	Mean % Mass	Rank
Echinoidea	46,15	24,00	11,07
<i>Parechinus angulosus</i>	46,15		
Polychaeta	32,69	12,05	3,94
<i>Lysidice natalensis</i>	7,79		
<i>Lepidonotus semitectus</i>	5,76		
<i>Pseudonereis variegata</i>	3,84		
<i>Cirriformia capensis</i>	1,92		
<i>Gunnarea capensis</i>	1,92		
Asciacea	19,23	12,69	2,44
<i>Pyura stolonifera</i>	11,53		
Anthozoa	21,15	10,12	2,14
<i>Bunodactis reynaudi</i>	9,61		
<i>Bunodosoma capensis</i>	3,84		
Rhodophyta	28,84	4,25	1,22
<i>Duthiophycus setchelli</i>	9,61		
<i>Polysiphonia</i> sp.	5,76		
<i>Arthrocardia</i> sp.	5,76		
<i>Hypnea</i> spp.	3,84		
<i>Amphiroa ephedraea</i>	1,92		
<i>Gelidium amansii</i>	1,92		
<i>Porphyra capensis</i>	1,92		
<i>Champia compressa</i>	1,92		
<i>Jania</i> sp.	1,92		
<i>Corallina</i> sp.	1,92		
Bivalvia	17,30	5,61	0,97
<i>Perna perna</i>	15,38		
Gastropoda	19,23	4,88	0,93
<i>Patella</i> spp.	5,76		
<i>Amblychilepas scutellum</i>	3,84		
<i>Gibbula zonata</i>	1,92		
<i>Fissurella mutabilis</i>	1,92		
Cephalopoda	11,53	7,76	0,89
<i>Octopus vulgaris</i>	9,61		
Cirripedia	9,61	4,69	0,45
<i>Balanus</i> spp.	9,61		
Amphipoda	15,38	2,54	0,39
Gammaridea	11,53		
Caprellidea	1,92		
Chlorophyta	19,23	1,88	0,36
<i>Ulva</i> spp.	13,46		
<i>Bryopsis</i> spp.	7,69		
Decapoda	17,30	1,40	0,24
<i>Plagusia chabrus</i>	9,61		
Bryozoa	15,38	0,51	0,07
Insecta	3,84	0,78	0,03
Isopoda	7,69	0,30	0,02
Holothuroidea	5,76	0,38	0,02
<i>Pentacucumis</i>			
<i>spyriddophora</i>	1,92		
Asteroidea	1,92	0,59	0,01
<i>Patiriella</i> sp.	1,92		
Porifera	1,92	0,25	T
Pisces	1,92	0,25	T
Ophiuroidea	1,92	0,09	T
<i>Ophionereis porrecta</i>	1,92		
Hydrozoa	1,92	0,01	T
Unidentified	13,46	4,86	0,65

Trace (T) = Items with a rank of less than 0,01

1986) where algae was found to be an important dietary component of *D. sargus*.

Diet of *D. cervinus*

Juvenile *D. cervinus* had a more solitary habit, seldom being observed with more than four individuals in a loose group. They were secretive and often found near the bottom of rock pools or sublittoral areas in close association with cover. Amphipods and polychaete worms were the major prey items in the diet of the 23 juvenile *D. cervinus* (32–150 mm FL) sampled (Table 4). As found by Christensen (1978), small juveniles (32–50 mm FL) fed mainly on chironomid larvae (*Telmatogeton minor*) and harpacticoid copepods. Amphipods and polychaetes then became successively more important in the diet of the juveniles (51–150 mm FL), which

Table 4

Stomach content analysis of juvenile *Diplodus cervinus hottentotus* between 32 mm and 150 mm fork length, sampled by rotenone poisoning and spear in shallow subtidal waters in the TNP from April 1989 to December 1990 (n=23)

Prey Species	% Freq. Occ.	Mean % Vol.	Rank
Amphipoda	69,56	39,13	27,22
Gammaridea	69,56		
Caprellidea	13,04		
Polychaeta	39,13	28,73	11,24
<i>Lysidice natalensis</i>	8,69		
Insecta	8,69	5,86	0,51
<i>Telmatogeton minor</i>	8,69		
Bivalvia	8,69	4,56	0,39
Isopoda	8,69	3,04	0,26
<i>Dynamenella</i> spp.	4,34		
Copepoda	8,69	2,60	0,22
Harpacticoida	8,69		
Tanaidacea	13,04	0,86	0,11
<i>Apseudes</i> spp.	13,04		
Decapoda	4,34	0,21	T
Gastropoda	4,34	0,21	T
Pisces	4,34	0,17	T
Scales	4,34		
Anthozoa	4,34	0,15	T
Ostracoda	4,34	0,04	T
Bryozoa	4,34	0,04	T
Mysidacea	4,34	0,04	T
Hydrozoa	4,34	0,02	T
Unidentified	30,43	13,82	4,20

Trace (T) = Items with a rank of less than 0,01

Table 5

Stomach content analysis of sub-adult *Diplodus cervinus hottentotus* between 151 mm and 300 mm fork length, sampled in the TNP from April 1989 to December 1990 (n=91)

Prey Species	% Freq. Occ.	Mean % Mass	Rank
Polychaeta	82,41	61,22	50,46
<i>Lysidice natalensis</i>	27,47		
<i>Sepula vermicularis</i>	14,28		
<i>Lepidonotus semitectus</i>	13,18		
<i>Cirriiformia capensis</i>	13,18		
<i>Gunnarea capensis</i>	7,69		
<i>Euphrosine capensis</i>	4,39		
<i>Pista</i> spp.	3,29		
<i>Thelepus</i> spp.	3,29		
<i>Pseudonereis variegata</i>	1,09		
Amphipoda	60,43	11,78	7,11
Gammaridea	54,94		
<i>Paramoera capensis</i>	13,18		
<i>Ceradocus</i> spp.	4,39		
Caprellidea	10,98		
Echinoidea	17,58	4,17	0,73
<i>Parechinus angulosus</i>	17,58		
Ophiuroidea	17,58	3,50	0,61
<i>Ophiocoma valenciae</i>	2,19		
<i>Ophiothrix fragilis</i>	1,09		
Sipunculida	18,68	1,90	0,35
<i>Phascolosoma japonicum</i>	18,68		
Decapoda	10,98	2,92	0,32
<i>Plagusia chabrus</i>	2,19		
Gastropoda	14,28	2,06	0,29
<i>Haliotis spadicea</i>	3,29		
<i>Fissurella mutabilis</i>	3,29		
<i>Littorina</i> spp.	2,19		
<i>Gibbula capensis</i>	1,09		
Isopoda	9,89	1,45	0,14
<i>Dynamenella</i> spp.	3,29		
<i>Mesanthura catenula</i>	2,19		
Asciadiacea	2,19	1,54	0,03
<i>Pyura stolonifera</i>	2,19		
Holothuridae	4,39	0,60	0,02
Cirripedia	2,19	1,14	0,02
<i>Balanus venustus</i>	1,09		
Bivalvia	5,49	0,24	0,01
<i>Perna perna</i>	2,19		
Pisces	4,39	0,27	0,01
Scales	4,39		
Mysidacea	3,29	0,27	T
<i>Gastrosaccus?</i> sp	2,19		
Rhodophyta	4,39	0,18	T
<i>Acrosorium maculatum</i>	1,09		
<i>Plocamium rigidum</i>	1,09		
Nematoda	1,09	0,38	T
Hydrozoa	2,19	0,04	T
Anthozoa	2,19	0,02	T
Insecta	1,09	0,04	T
Tanaidacea	1,09	0,02	T
Polyplacophora	1,09	0,01	T
Unidentified	9,89	6,03	0,59

Trace (T) = Items with a rank less than 0,01

Table 6

Stomach content analysis of adult *Diplodus cervinus hottentotus* between 301 mm and 440 mm fork length, sampled in the TNP and adjacent areas from April 1989 to December 1990 (n=36)

Prey Species	% Freq. Occ.	Mean % Mass	Rank
Amphipoda	83,33	21,84	18,20
Gammaridea	72,22		
<i>Paramoera capensis</i>	22,22		
<i>Ceradocus</i> spp.	5,55		
Caprellidea	22,22		
<i>Caprella</i> sp.	5,55		
Polychaeta	72,22	23,93	17,28
<i>Lysidice natalensis</i>	16,66		
<i>Lepidonotus semitectus</i>	11,11		
<i>Euphrosine capensis</i>	5,55		
<i>Cirriiformia capensis</i>	5,55		
<i>Eunice</i> sp.	5,55		
Nereidae	5,55		
<i>Serpula vermicularis</i>	2,77		
<i>Syllis</i> sp.	2,77		
<i>Nicolea macrobranchia</i>	2,77		
<i>Gunnarea capensis</i>	2,77		
<i>Loimia medusa</i>	2,77		
Decapoda	61,11	14,70	8,98
<i>Plagusia chabrus</i>	27,77		
<i>Eriphia smithii</i>	5,55		
<i>Mursia cristimanus</i>	2,77		
Ophiuroidea	52,77	12,09	6,38
<i>Ophiothrix fragilis</i>	8,33		
<i>O. trigrochis</i>	2,77		
Echinoidea	38,88	6,45	2,51
<i>Parechinus angulosus</i>	38,88		
Gastropoda	36,11	5,15	1,86
<i>Fissurella mutabilis</i>	22,22		
<i>Gibbula zonata</i>	16,66		
<i>Haliotis spadicea</i>	13,88		
<i>Amblychilepas scutellum</i>	8,33		
Isopoda	33,33	2,56	0,85
<i>Dynamenella</i> spp.	22,22		
Sipunculida	19,44	2,02	0,39
<i>Phascolosoma japonicum</i>	19,44		
Asciadiacea	8,33	4,27	0,35
<i>Pyura stolonifera</i>	8,33		
Cephalopoda	8,33	3,05	0,25
<i>Octopus vulgaris</i>	5,55		
Pisces	11,11	0,50	0,05
<i>Chorisochismus dentex</i>	2,77		
Holothuridae	5,55	0,52	0,02
<i>Pentacta doliolum</i>	2,77		
Anthozoa	11,11	0,25	0,02
<i>Bunodactis reynaudi</i>	5,55		
Bivalvia	11,11	0,15	0,01
<i>Perna perna</i>	5,55		
Pycnogonida	8,33	0,18	0,01
Asteroidea	2,77	0,33	T
<i>Patiriella exigua</i>	2,77		
Polyplacophora	5,55	0,12	T
<i>Chiton tulipa</i>	2,77		

Table 6 cont/...

Table 6 (continued)

Prey Species	% Freq. Occ.	Mean % Mass	Rank
Rhodophyta	5,55	0,04	T
<i>Gelidium amansi</i>	2,77		
<i>Corallina</i> sp.	2,77		
Cirripedia	5,55	0,02	T
Bryozoa	2,77	0,01	T
Unidentified	8,33	1,72	0,14

Trace (T) = Items with a rank of less than 0,01

tended to be less secretive and to forage as searchers (Hughes 1980).

Sub-adult *D. cervinus* (151–300 mm FL) occurred on inshore reefs in a similar habitat to, and often together with *D. sargus*. Polychaete worms and amphipods were the most important items in their diet and overall diversity in the diet was low (Table 5). This feeding specialisation is reflected in the functional anatomy of the mouth, thick lips and fine incisiform teeth enabling them to capture prey such as the polychaete *Lysidice natalensis*, which burrows under *Pyura* pods (Day 1974). Amphipods, particularly benthic gammarids such as *Paramoera capensis* and caprellids were also taken in large numbers.

Adult *D. cervinus* (301–440 mm FL) were also found alone or in small aggregations of up to five individuals. They were furtive in habit and frequently observed in close association with caves or boulder strewn gullies on high relief reefs down to about 25 metres. Although their diet consisted predominantly of polychaetes and amphipods, they consumed a larger spectrum of prey organisms than did the sub-adults (Table 6). Other important groups included decapod crustaceans such as the rock crab, *Plagusia chabrus* and ophiuroids such as *Ophiothrix fragilis*. The ingestion of these and other prey species such as urchins and gastropods suggest that adult *D. cervinus* have a greater ability than sub-adults to manipulate certain prey both in terms of capture and mastication.

Dietary overlap and seasonality

A comparison between *D. sargus* and *D. cervinus* revealed a significant overlap in the diets of juveniles ($r_s = 0,591$) and sub-adults ($r_s = 0,593$, $P < 0,01$) both of which preyed extensively on small amphipods. Overlap in the diet of adult fish was not significant ($r_s = 0,297$ $P > 0,05$) because *D. sargus* switched to larger prey including polychaetes, echinoids and ascidians while *D. cervinus* retained a preference for small prey including amphipods and polychaetes.

Seasonal changes in the diet of *D. sargus* are shown in Figure 4. A clear shift in diet was apparent with amphipods making up 39,5% (RI) of their diet during the winter and only 8,7% (RI) in summer. During summer, anthozoans, ascidiaceans, gastropods and algae were more important in their diet. This difference was most noticeable in juvenile *D. sargus* in which amphipods made up a major proportion (93% RI) of their winter diet. In summer they were partially replaced by polychaetes, harpacticoid copepods and *Telmatogeton* larvae.

A similar trend was observed in *D. cervinus* (Fig. 5). In winter amphipods constituted 30,2% (RI) of their diet decreasing to 17,4% (RI) during the summer months during which polychaetes and decapod crustaceans were more important. The amphipods preyed upon by both species consisted of a number of species, most belonging to the families Eusiridae, Gammaridae and Caprellidae. The most important species were *Paramoera capensis* and *Caprella* spp. which are abundant epifaunal carnivores (Griffiths 1976) and may be found living in association with seaweeds on rocky shores (Branch & Branch 1981). The data suggest an increase in the abundance and/or availability of these amphipods in winter. There is however, no record of seasonal fluctuation in the abundance of benthic amphipods along the coast of southern Africa and little is known about the biology of individual species (Prof. C.L. Griffiths, University of Cape Town, *pers. comm.*). Alternatively it may be an indication

that the fish move inshore during winter, feeding predominantly on nearshore algal beds.

Discussion

Analysis of the stomach contents of *D. sargus* sampled in the Tsitsikamma area showed that they were benthic omnivores, feeding on a wide variety of prey associated with inshore reefs. A comparison of this data and studies on the diet of juvenile *D. sargus* from different habitats on the South African coast showed that although a certain degree of trophic plasticity existed, major prey items were similar. These included small crustaceans, chlorophytes and polychaetes (Christensen 1978; Joubert & Hanekom 1980; Whitfield 1985; Lasiak 1986). A significant difference between this study and those reported in the literature was the relative unimportance of algae in the diet of fish in the Tsitsikamma. The small percentage of algae in the diet suggested accidental ingestion. The importance of macro-algae *per se* in the diet of fish sampled elsewhere has not been demonstrated, Joubert & Hanekom (1980) suggesting that the fish were cropping epiphytic diatoms from the algal surface.

In rock pools and in shallow subtidal areas seaweeds serve as micro-habitats for a diverse and abundant epifauna (Branch & Branch 1981). They are thus important foraging grounds for juvenile fishes as was observed in the Tsitsikamma. The increased importance of algae in the diet of *D. sargus* living in the sandy surf zone and in estuaries suggests that, in the absence of preferred animal prey, they are capable of obtaining nutrients either from the weed itself or from epiphytic organisms. This dietary width must certainly contribute to the success of these fish in such differing habitats. With increasing size *D. sargus* changed from being planktonic feeders as small juveniles, to benthic browsing as adults. This coincided with the development of a more robust dentition and an increasing number of molars in the upper and lower jaws. The large diversity of prey found in the diet of sub-adult and adult fishes

also emphasised the generalist nature of the species.

By comparison *D. cervinus* was more of a specialist with a more restricted diet than *D. sargus*. The absence of algae in the stomachs of juveniles and its presence only as trace amounts in the stomachs of sub-adult and adult fish, showed that they were carnivorous. *D. cervinus* showed a preference for small, soft-bodied prey items, primarily polychaetes and amphipods, which together made up 95% of their diet. This was also evident in the functional morphology of their mouths, relatively few molars, narrow forward projecting incisors and fleshy lips indicating that they were pickers. Unlike other sympatric sparid species such as *Chrysoblephus laticeps* (Buxton 1984) and *Sparodon durbanensis* (Buxton & Clarke 1991) and *D. sargus*, *D. cervinus* did not appear to switch to larger prey with increasing size. The observation by Van der Elst (1981) that *D. cervinus* switched from a carnivorous diet as juveniles to a herbivorous diet as adults was not evident in this study.

A significant dietary overlap was evident in juvenile *D. sargus* and *D. cervinus*, both feeding predominantly on gammarid and caprellid amphipods. Although juvenile *D. sargus* were far more abundant in tidal rock pools and subtidal gullies than juvenile *D. cervinus* (Burger 1991), dietary overlap is a measure of similarity, not an indication of competition between the species (Hulbert 1978; Schoener 1983). Burger (1991) found that benthic amphipods were important to the diet of 18 other littoral fish species inhabiting tidal rock pools and subtidal gullies in the Tsitsikamma. While none of these studies were able to identify amphipods to species level or demonstrate possible spatial or temporal aspects of the utilisation of this resource, they illustrate a high usage of a common food resource and the importance of amphipods to the food chain.

In summary, dietary analysis in *D. sargus* showed that they were generalist, benthic omnivores feeding opportunistically on a wide variety of prey. This is thought to con-

tribute to their ability to inhabit a range of habitats including estuaries, sandy surf zones and inshore reefs and to their relatively high numbers in these areas. On the other hand *D. cervinus* is more of a specialist with a narrow dietary width and is found in smaller numbers on subtidal reefs.

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