Ontogenetic and seasonal shifts in the diet of *Diplodus cervinus hottentotus* (Pisces: Sparidae) in southern Angola

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Dietary information on the zebra seabream *Diplodus cervinus hottentotus* was collected between March 2011 and February 2012 in southern Angola. Invertebrates dominated the diet of *D. c. hottentotus* (61.08% ranking index [RI]) and comprised Polychaeta (38.9% RI), Amphipoda (13.2% RI), Cirripedia (2.5% RI) and Bivalvia (1.9% RI). Although there was no general ontogenetic shift in diet, the diet of larger fish did include larger, more robust prey items such as brachyurans and gastropods. Dietary diversity as well as feeding intensity peaked during autumn and winter, a possible consequence of the intrusion of nutrient-rich Benguela Current water, as well as the onset of reproduction during this period. *Diplodus cervinus hottentotus* from southern Angola shared a very similar diet to that of conspecifics in South African waters, but the diet differed considerably from that recorded in *D. c. cervinus* from the coast of Algeria in the Mediterranean Sea.

Keywords: Benguela, diet, polychaete

Introduction

Fishes of the family Sparidae occupy a diverse range of trophic niches, from herbivores to generalist omnivores and specialist predators (Hanel and Tsigenopoulos 2011). Feeding specialisation in this family is facilitated by diversity in tooth type and anterior jaw arrangement (Vandewalle et al. 1995). Other fish families, such as Cyprinidae and Labridae, have developed crushing pharyngeal teeth to process their food. Sparids, however, have retained a simple pharyngeal tooth arrangement and instead have developed molariform teeth to process hard-shelled molluscs and invertebrate prey. Hanel and Tsigenopoulos (2011) suggested that this alternate strategy is a major factor facilitating the trophic diversity in sparid fishes.

Some sparids have specialised their feeding mode to utilise vacant, or underutilised, trophic niches (for example, in species that feed on hard-shelled molluscs), thus avoiding feeding competition with other species (Wassef and Eisawy 1985; Buxton and Clarke 1991). In resource-limited environments, these adaptations can give a population an advantage over competitors, but adaptations such as dentition or head shape can also provide clues to what prey items can be consumed by fishes (Wainwright 1988). Trophic morphology, however, is often a deeply fixed phylogenetic trait that may not actually represent a corresponding diet in the immediate environment (Wainwright and Richard 1995). Diet is more often related to the immediately available prey items that provide the most energy at the least cost (Emlen 1966; MacArthur and Pianka 1966). For example, *Pagellus erythrinus* has a jaw with large crushing molars that are well adapted for crushing hard prey items. Unsurprisingly, this species feeds on hard-shelled

brachyurans (Caragitsou and Papaconstantinou 1985), but in certain habitats its dominant prey items are soft-bodied polychaetes (Jukic 1972). Thus, the functional foraging morphology, such as tooth or mouth shape, is not always a good predictor of the trophic niche occupied by a species. Consequently, if dietary differences are found within a species, these may be driven by extrinsic ecological factors (e.g. competition or resource availability) (Hernandez and Motta 1997).

The diet of the zebra seabream *Diplodus cervinus hottentotus* in South African waters has been described in two studies. Christensen (1978) studied the diet of the early life-history stages, whereas Mann and Buxton (1992) assessed the feeding biology of juveniles and adults in a no-take marine protected area. A feeding study has been conducted on *Diplodus cervinus cervinus* in the southern Mediterranean Sea off the coast of Algeria (Derbal and Kara 2006). Both of the South African studies concluded that juveniles (<100 mm fork length [FL]) feed predominantly on small invertebrates such as chironomid larvae and polychaete worms. Mann and Buxton (1992) concluded that adults were generalist invertebrate predators that fed primarily on polychaetes and amphipods. Derbal and Kara (2006), however, found that *D. c. cervinus* was a generalist omnivore that fed predominantly on carid shrimps and other invertebrates, but that also preyed on benthic macrophytes. Both Derbal and Kara (2006) and Mann and Buxton (1992) suggested that larger fish (>301 mm FL) were more opportunistic and preyed on larger food items.

Trophic seasonality in benthic reef fishes is well known. For example, in a study carried out on *Pagrus auratus* in

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New Zealand waters, Kingett and Choat (1981) found a shift from amphipods in summer to bivalves and polychaetes in winter, and a significant decrease in feeding intensity in winter. Denny and Schiel (2001) observed changes in feeding intensity in *Notolabrus fucicola* and attributed this to reduced water temperatures and the onset of reproduction in winter. Similar trophic seasonality in the *D. cervinus* species complex, in terms of feeding intensity, has been recorded in Algerian waters, with the highest intensity observed during spring, but there was very little seasonal change in terms of dietary composition (Derbal and Kara 2006). Conversely, in South African waters, there was no clear seasonal change in feeding intensity but a marked shift in prey selectivity (Mann and Buxton 1992).

The southern Angolan region's coastal climate changes dramatically between winter and summer, being influenced by the warm, southward-flowing, oligotrophic, equatorial Angola Current during summer and the cooler, northward-flowing, eutrophic, temperate Benguela Current during winter. This seasonal variation may have an influence on food availability, which may in turn be reflected in the diet of *D. c. hottentotus*. Richardson et al. (2011), who studied the congeneric *Diplodus sargus capensis* population in southern Angola, found that feeding intensity did not vary seasonally. However, algae were more important in the diets of these fish during winter, a possible influence of the nutrient-rich Benguela Current.

This study aims to describe the diet of *D. c. hottentotus* in southern Angola, with a focus on how size and season may affect dietary composition and feeding intensity. The disjunct distribution of the *Diplodus cervinus* species complex between the coastal temperate waters of the Mediterranean (*D. c. cervinus*) and south-eastern and south-western Africa (*D. c. hottentotus*) offers an opportunity to assess comparatively the effects of different habitats and allopatry on diet.

Material and methods

Study location

Fish were sampled along a 28 km section of coastline between Namibe and Tombua in the Namibe province of Angola (Figure 1). The coastal marine environment is comprised of intermittent, fissured, medium-profile sandstone reef between areas of sand. Although the region is located within the tropics, it is characterised by a temperate climate, a consequence of the Angola–Benguela Frontal Zone (ABFZ). The ABFZ is formed by the convergence of the cool, northward-flowing Benguela Current and the warm, southward-flowing Angola Current. During winter, the front is shifted northwards by the dominating Benguela Current, bringing cooler water to the study site. In summer, when the Angola Current is dominant, the front is displaced southwards, resulting in increasing water temperatures in the study area (Meeuwis and Lutjeharms 1990).

General methods and description of diet

A total of 190 *D. c. hottentotus* were collected using a speargun in the inshore zone (0–15 m depth) between March 2011 and February 2012. Fish were weighed to the nearest 0.1 g and measured (FL, mm). Stomachs were

removed – by severing the oesophagus at the buccal cavity and at the intestine immediately anterior to the pyloric caecae – and stored in 10% formalin for later laboratory analysis. The eviscerated mass of fish (without internal organs) was then weighed to the nearest 0.1 g.

In the laboratory, stomachs were dissected and the contents weighed. Individual food items were identified to the lowest possible taxon – using a dissecting microscope – and weighed to the nearest 0.0001 g, after excess fluid had been drawn from the sample using absorbent blotting paper. In cases where food items were inseparable, the proportion of each food type was estimated visually and multiplied by the total mass of the conglomerate.

The importance of each food item was quantified using the frequency of occurrence (% of stomachs containing a specific food item; %F) and percentage mass (mass of each food category expressed as a percentage of the total mass of the contents of all stomachs; %M) (Berg 1979). The relative importance of each food item was assessed using the ranking index (RI) method, which was calculated as the product of the frequency of occurrence (%F) and the percentage mass (%M) (Hobson 1974). Fish were split into small (<225 mm FL, 0–50% maturity), medium (225–275 mm FL, 51–99% maturity) and large (>275 mm FL, 100% maturity) (Winkler 2013). In order to compare the relative importance of food items between size classes, the RI for each food item was expressed as a percentage of the sum of the RI values for all food items within a specific size class of fish (%RI). The stomachs of fish in all size classes contained large amounts of sand and unidentified matter. Most of the unidentified matter was recognisable as partially digested prey, such as shell fragments or flesh, and therefore contributed nutritionally to the fish and was subsequently included in analyses. Some of this matter,
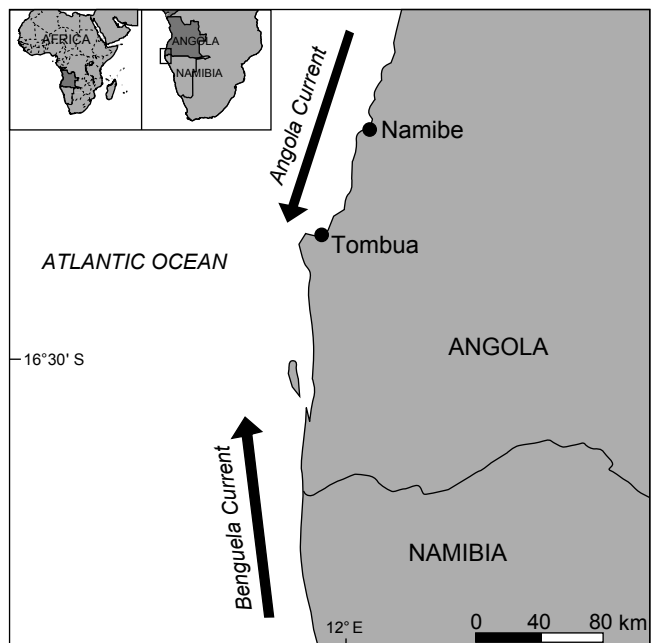
Figure 1: Map of southern Angola showing places mentioned in text

however, comprised white gelatinous material, which was probably stomach lining and was thus excluded from the analysis. As sand is inert and non-nutritive, it was also excluded from any analysis.

To test for similarity in dietary composition between size classes, the mass contribution of each prey category was square-root transformed and subjected to a Bray–Curtis similarity analysis (Bray and Curtis 1957). The similarities in diet between the size classes were illustrated by means of dendrograms and tested for differences using an analysis of similarity (ANOSIM) presumption test (Clarke and Warwick 1994), using the statistical package PAST Version 2.16 (Hammer et al. 2001). The difference between size classes was considered significant at $p < 0.05$. The significance of the ANOSIM results was based on the R-statistic, where values of R usually range between zero and one. A value of zero indicates that the similarities between and within size classes are the same, whereas a value of one suggests that all replicates within size classes are more similar to each other than to any replicates from other size classes.

Feeding seasonality

Descriptive seasonal variation in the dietary composition of *D. c. hottentotus* was assessed by comparing the stomach contents and the %RI between autumn (February–April), winter (May–July), spring (August–October) and summer (November–January). Similarities in the dietary composition between seasons were analysed in the same way as between size classes and were illustrated using dendrograms.

Feeding intensity

Feeding intensity between seasons and size classes was assessed using a stomach fullness index (SFI) (Man and Hodgkiss 1977), calculated as:

$$\text{SFI} = \frac{\text{Stomach content mass}}{\text{Eviscerated fish mass}} \times 100$$

The effect of season and size class on feeding intensity was tested using a two-way ANOVA and differences in sample means were considered significant at $p < 0.05$.

Results

Relative importance of prey items

Of the 190 *D. c. hottentotus* stomachs examined, only 31 (16.3%) were empty and hence excluded from the analysis. Invertebrate prey items (61.08% RI) dominated the overall diet and included Polychaeta (38.88% RI), Amphipoda (13.21% RI), Cirripedia (2.55% RI) and Bivalvia (1.86% RI) (Table 1).

Larger prey items, such as Brachyura, Pisces, Anomura, Gastropoda and Cephalopoda, were either absent or present in very low numbers in the stomachs of the small individuals, but were fairly well represented in the diets of larger fish (Table 1). The stomachs of fish in all size classes

Table 1: The relative importance of different prey taxa to the overall diet as well as the diet of small (<225 mm), medium (225–275 mm), and large (>275 mm) *Diplodus cervinus hottentotus* from southern Angola. The four most important prey items per predator category are shown in bold. %*F* = percentage frequency of occurrence, %*M* = percentage mass, %*RI* = percentage ranking index

Prey item	All (n = 159)			Small (n = 35)			Medium (n = 83)			Large (n = 41)		
	%*F*	%*M*	%*RI*	%*F*	%*M*	%*RI*	%*F*	%*M*	%*RI*	%*F*	%*M*	%*RI*
Annelida												
Polychaeta	66.67	27.79	**38.88**	57.14	30.81	**35.53**	71.08	26.53	**35.19**	65.85	27.76	**44.32**
Arthropoda												
Amphipoda	72.33	8.71	**13.21**	57.14	3.71	**4.28**	83.13	10.73	**16.64**	63.41	8.88	**13.65**
Cirripedia	23.27	5.22	**2.55**	2.86	0.26	0.01	26.51	5.62	**2.78**	34.15	8.63	**7.14**
Caridae	16.98	4.27	1.52	8.57	3.20	0.55	15.66	4.25	1.24	26.83	5.22	3.40
Brachyura	16.35	4.06	1.39	–	–	–	20.48	4.61	**1.76**	21.95	6.41	3.41
Tanaidacea	18.87	0.91	0.36	28.57	3.46	**2.00**	18.07	0.20	0.07	12.20	0.15	0.04
Isopoda	13.21	0.34	0.09	5.71	0.62	0.07	16.87	0.27	0.08	12.20	0.24	0.07
Anomura	2.52	1.27	0.07	–	–	–	4.82	2.43	0.22	–	–	–
Mysidacea	3.14	0.72	0.05	–	–	–	3.61	0.16	0.01	4.88	2.48	0.29
Insecta	0.63	<0.01	<0.01	–	–	–	–	–	–	2.44	<0.01	<0.01
Mollusca												
Bivalvia	23.27	3.81	**1.86**	14.29	5.46	**1.57**	18.07	2.13	0.72	41.46	5.82	**5.85**
Gastropoda	15.72	1.29	0.43	–	–	–	16.87	1.64	0.52	26.83	1.68	1.09
Polyplacophora	11.95	1.53	0.38	5.71	4.50	0.52	13.25	0.61	0.15	14.63	0.85	0.30
Cephalopoda	1.89	1.41	0.06	–	–	–	2.41	1.58	0.07	2.44	2.28	0.13
Plantae												
Chlorophyta	18.87	3.71	1.47	14.29	3.74	1.08	16.87	4.28	1.35	26.83	2.54	1.65
Rhodophyta	7.55	2.22	0.35	2.86	2.86	0.16	6.02	1.39	0.16	14.63	3.37	1.19
Other												
Pisces	8.81	3.19	0.59	5.71	0.09	0.01	7.23	0.73	0.10	14.63	10.80	3.83
Bryozoa	5.66	1.04	0.12	8.57	0.33	0.06	4.82	1.77	0.16	4.88	0.15	0.02
Holothuroidea	7.55	0.68	0.11	2.86	0.12	<0.01	10.84	0.64	0.13	4.88	1.22	0.14
Ophiuroidea	1.26	0.06	<0.01	–	–	–	2.41	0.11	<0.01	–	–	–
Unidentified	62.89	27.66	36.51	65.71	40.84	54.15	68.67	30.16	38.64	48.78	11.37	13.44

SIZE CLASS (mm)
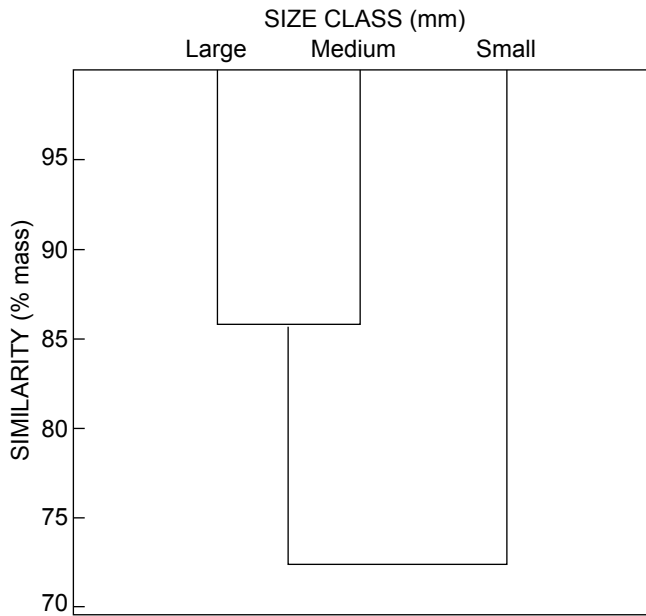
Figure 2: Similarity dendrogram of the dietary composition of small (<225 mm), medium (225–275 mm) and large (>275 mm) *Diplodus cervinus hottentotus* in southern Angola

contained large amounts of unidentifiable organic matter (Table 1).

The composition of the diet of small fish (<225 mm) was 73.1% similar to the diets of the large (>275 mm) and medium (225–275 mm) fish combined, whereas the diets of large and medium fish were more similar to each other (86% similarity index) (Figure 2). The ANOSIM indicated that the Bray–Curtis clusters were significantly different from one another ($R = 0.09$, $p < 0.01$). However, the low R-value indicated that there was a large degree of similarity between the clusters.

Feeding seasonality

Polychaetes were the dominant identified prey in all seasons, especially during autumn (51.1% RI), winter (37.2% RI) and spring (35.6% RI) (Figure 3). Amphipods were also well represented during all seasons, except autumn (3.9% RI). The diets were the most diverse in autumn and winter when prey items other than polychaetes and amphipods comprised over 30% of the total RI (Figure 3). Unidentifiable organic matter increased through the seasons: 6.5% (autumn); 20.2% (winter); 50.1% (spring); and 68.6% in summer (Figure 3).

In terms of mass, the dietary composition of *D. c. hottentotus* in the autumn/winter period was 65.2% similar to that in the spring/summer period (Figure 4). The diets of these fish were slightly less similar between autumn and winter
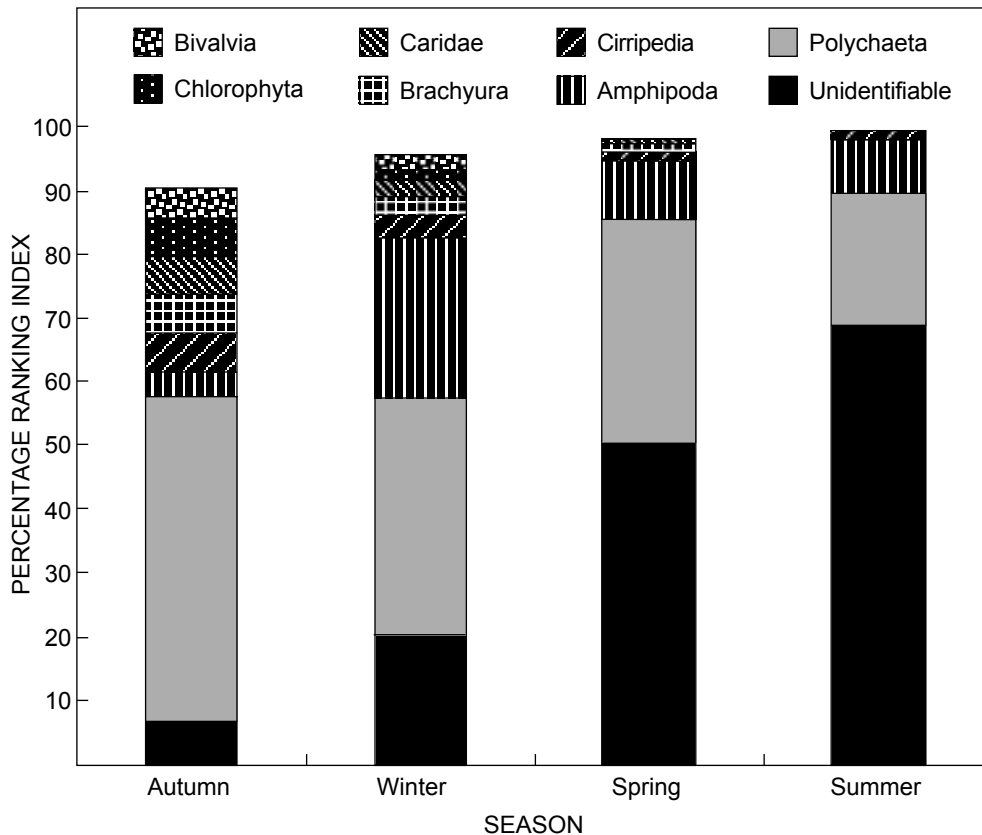
Figure 3: Seasonal percentage ranking index (%RI) for the dietary items found in the stomachs of *Diplodus cervinus hottentotus* in southern Angola between March 2011 and February 2012

than between spring and summer (78.5% and 81.1% respectively; Figure 4). The ANOSIM results indicated that the Bray–Curtis clusters were significantly different from one another ($R = 0.09$, $p < 0.01$). However, the low R-value indicated that there was a large degree of similarity between the clusters.

Feeding intensity

There was no significant interaction between season (ANOVA: $F_{(3,146)}$, $p = 0.43$) and size class (ANOVA: $F_{(2,146)}$, $p = 0.07$) in relation to SFI (Figure 5). The mean seasonal feeding intensity during winter and spring was generally greater than during summer and autumn (Figure 5).

Discussion

Diplodus cervinus hottentotus in southern Angola occupies a benthivorous niche, consuming mainly invertebrates. Although there were small changes in the contribution of certain prey items between size classes, the two main food groups, polychaetes and amphipods, were the most important prey in all three size classes. This diet was very similar to that of the *D. c. hottentotus* population found along the south-east coast of South Africa (Mann and Buxton 1992). In contrast, the feeding habits of this population were very different to those of *D. c. cervinus* off the coast of Algeria in the southern Mediterranean, which, although also occupying a benthivorous niche, fed mainly on hard-bodied caridean shrimps and bivalves (Derbal and Kara 2006).

Differences in the stomach contents of the Algerian population compared to those in southern Africa may be attributed to both sampling bias and prey availability, where

the latter is associated with prey density, prey habitat utilisation and the ability of the forager to access the prey item, i.e. trophic morphology.

In the present study, and that of Mann and Buxton (1992), shallow-water (0–15 m) spearfishing was the main sampling technique used in the collection of *D. c. hottentotus*. In the study by Derbal and Kara (2006), the fish were collected mainly with passive gear (gillnets and longlines). Such gear is associated with a range of potential biases in feeding studies, including post-capture digestion, regurgitation and selectivity (Hyslop 1980). Post-capture digestion can cause over- and underestimation of hard- and soft-bodied prey items respectively. Regurgitation, while unavoidable in both active and passive methods, is thought to be higher using passive gear because of the often-longer period of time taken for a fish to die after capture (Bowen 1996). Passive gear is also more likely to capture moving, hungry fish, which are more likely to have digested much of the food in their stomachs. This is particularly the case for easily digestible prey items. In a critique of feeding studies in fish, Vinson and Angradi (2011) found that the average percentage of fish with empty stomachs that were caught using passive gear was 35.9%, compared with 21.7% when using active gear.

Shallow-water spearfishing as a sampling method in feeding studies, therefore, is not directly comparable to passive capture methods. Using spearfishing, death is instantaneous – which results in reduced post-capture digestion and regurgitation – and actively foraging fish are not selected. Spearfishing, however, has been criticised as a collection method by Vignon and Dierking (2011), who suggested that post-capture regurgitation may be increased when samples are brought up from depth and the
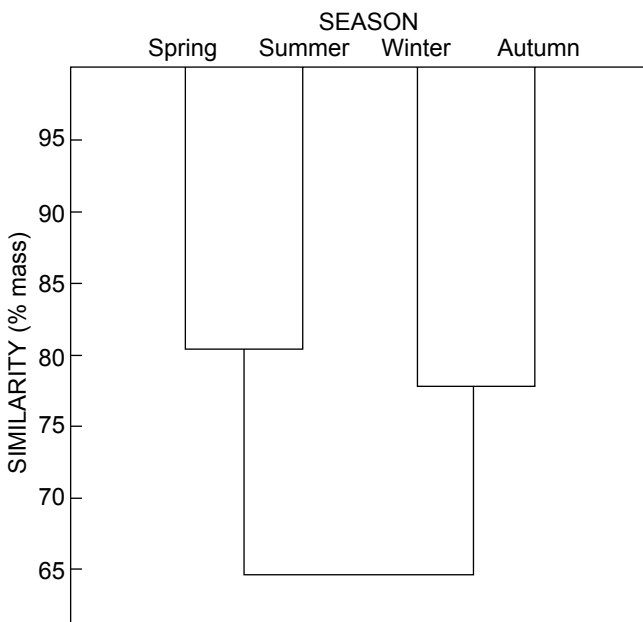
Figure 4: Similarity dendrogram of the seasonal dietary composition of *Diplodus cervinus hottentotus* in southern Angola
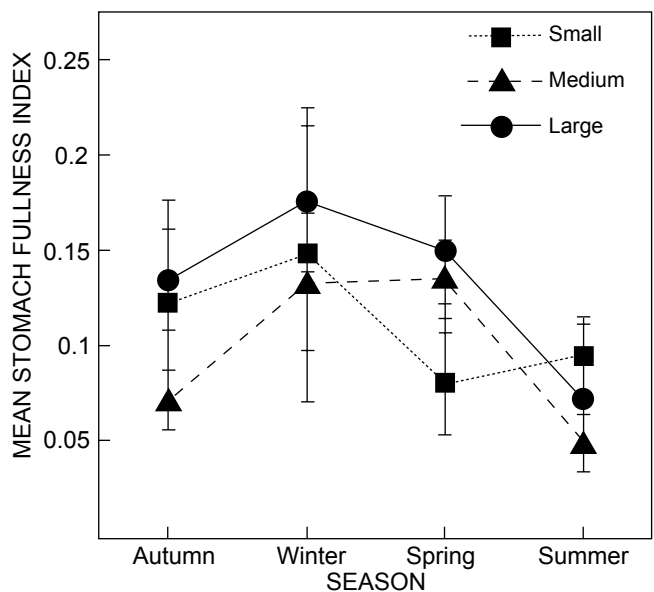
Figure 5: Comparison of the mean seasonal stomach fullness index of small (<225 mm FL), medium (225–275 mm FL) and large (>275 mm FL) *Diplodus cervinus hottentotus* in southern Angola. Error bars depict 95% confidence intervals

stomach is everted as a result of barotrauma. This concern, however, was based on fish that had been speared at depths >20 m, using SCUBA gear. In the present study, sampling occurred in waters <15 m, as was also the case in the study by Mann and Buxton (1992). Thus, the effects of barotrauma were not likely to have been a factor in either of these two studies. It is reasonable, therefore, to assume that the sampling methods used in the present study and that of Mann and Buxton (1992) provided a relatively unbiased description of the diet of *D. c. hottentotus*. Both of these studies suggest that *D. c. hottentotus* consumes large volumes of soft-bodied prey items, such as polychaetes, which were insignificant in the diet of *D. c. cervinus* (Derbal and Kara 2006).

Differences in prey availability are thought to influence the diet of other sparid fishes. Tancioni et al. (2003) found that the diet of *Sparus aurata* was more diverse in a more species-rich estuary (with high prey availability) compared to that of fish sampled from a neighbouring less-speciose estuary. The diet of juvenile *D. s. capensis* has been shown to vary among southern African marine habitats. Algae dominated the stomach contents of *D. s. capensis* in southern Angola (Richardson et al. 2011) and, in South Africa, in the Eastern Cape (Coetzee 1986) and KwaZulu-Natal (Joubert and Hanekom 1980). In another South African study, however, algae contributed little to the diet of that species along the Tsitsikamma coast, which is also in the Eastern Cape (Mann and Buxton 1992).

Unfortunately, there is limited habitat information in the Algerian study by Derbal and Kara (2006). However, some habitat variation is known to occur between the inshore zones of southern Angola and the Tsitsikamma coast, with the former characterised by scattered, low-profile reef (ACW pers. obs.) and the latter by continuous, high-profile reef (Buxton and Smale 1989). These habitat differences are probably a consequence of a relatively low-energy surf zone impacting the sandstone reef in southern Angola, compared with higher-energy conditions on the Tstitsikamma coast. Chen et al. (2002) documented an average wave height of approximately 3 m on the south-eastern coast of South Africa but an average of below 2 m in southern Angola. Although both these habitats are known to host populations of caridean shrimps (Mann and Buxton 1992; this study), which were important dietary items in the Algerian study, these do not appear to be abundant in either of these habitats (ACW pers. obs.). In addition, predatory and omnivorous fishes, such as juvenile *Argyrosomus coronus* (Potts et al. 2010), *Plectorhynchus mediterraneus* (WMP unpublished data), and *D. s. capensis* (Richardson et al. 2011), that occupy similar habitats in southern Angola, consumed these prey items in low numbers only, possibly suggesting limited availability.

Intraspecific dietary variation can often be attributed to prey density and the accessibility of the prey items to foraging individuals (Wootton 1998; Pita et al. 2002). Accessibility of prey is, in turn, dependent on whether the consumer is morphologically adapted to ingest the prey item in a particular environment (Hernandez and Motta 1997; Hanel and Tsigenopoulos 2011). For example, fish that lack crushing molars or robust pharyngeal teeth will not feed successfully on hard-shelled molluscs because they

are unable to manipulate the prey items into a manageable size that enables swallowing. Although trophic morphology data (shape and size of feeding apparatus) were unavailable for the *D. c. cervinus* population in Algeria, the species complex – which was split based on colouration – shows homologous morphology between subpopulations (Bauchot and Bianchi 1984). We thus assumed morphological homology between the Algerian and southern African subspecies. If this assumption holds true, differential prey availability is a more likely cause of the dietary differences observed in the Algerian population compared to the southern African populations.

When compared with *D. s. capensis*, which showed an ontogenetic shift from herbivory to durophagy (feeding on hard prey items) (Richardson et al. 2011), *Diplodus cervinus hottentotus* did not exhibit a clear ontogenetic dietary shift, with both polychaetes and amphipods being the most important prey items in all size classes. It is possible that the poor taxonomic resolution of the prey identification, which was hindered by a lack of published descriptions of the benthic invertebrate fauna of the region, may have masked a more subtle ontogenetic shift. However, as fish of all sizes were observed feeding in similar habitats during the sampling, this appears to be unlikely. Larger fish did, however, consume a wider range of prey items than did the smaller individuals. This included larger and more robust prey items, such as Brachyura, Pisces, Bivalvia and Cirripedia. This shift in dietary diversity was evident from the cluster analysis (Figure 2), which showed that the diets of medium and large fish were more similar to each other than to the diet of small fish. A similar trend was also observed in the South African population (Mann and Buxton 1992), but was less obvious in *D. c. cervinus* from the southern Mediterranean, probably due to the low occurrence of soft prey in all size classes. In that study, however, aquatic macrophytes were also included in the diet of larger fish (Derbal and Kara 2006). An ontogenetic shift towards larger prey items is not uncommon in fish (Karpouzi and Stergiou 2003), as is a shift towards more robust prey items in cases where the species in question is morphologically suited to a durophagous diet (Hernandez and Motta 1997; Richardson et al. 2012).

A shift in diet, from smaller and softer prey items to larger and harder items, is common in sparids (Buxton and Kok 1983; Buxton 1984; Buxton and Clarke 1986, 1989, 1991; Hernandez and Motta 1997; Fehri-Bedoui et al. 2009; Richardson et al. 2011). Hernandez and Motta (1997) assessed the possible morphological cause of this dietary shift in the sparid *Achosargus probatocephalus*. The authors found that the adjustment towards durophagy in this species was due to the development of robust crushing molars and increasing force generated by the abductor mandibular muscle complex (in the cheek) with increasing size. Similar findings were reported by Richardson et al. (2011) for *D. s. capensis* in southern Angola.

Seasonal variation in dietary composition is largely dependent on the seasonal availability of prey organisms (Wootton 1998) and reflects the adaptability of the consumer. Polychaetes and amphipods were the most important identifiable prey items in the diet of *D. c. hottentotus* in southern Angola, regardless of the season.

Although this suggests that there was little seasonal differentiation in the diet, again the possibility cannot be ruled out that low taxonomic resolution in the identification may have hidden subtle differences. There was, however, some variation in the relative importance of the general prey categories (Figure 3), which was reflected in the cluster analysis as being significant (Figure 4). The nutrient-rich Benguela Current dominates the southern Angolan region during autumn and winter and results in a peak in primary production (Meeuwis and Lutjeharms 1990), and this could potentially have an influence on benthic productivity, increasing the abundance of various invertebrate communities that occur in low numbers during the nutrient-deprived seasons of spring and summer. In addition, high nutrient levels in the food web could potentially reduce food competition between invertebrate communities, presenting a more diverse community of prey items to foraging fish. Experimentally induced water column eutrophication has produced similar effects on benthic freshwater invertebrate communities (Blumenshine et al. 1997).

In the present study, there were no significant changes in feeding intensity as a function of predator size or season. Feeding intensity was higher, however, during winter and spring, at the onset of the reproductive season of *D. c. hottentotus*, which extends from May to October (Winkler 2013), the period during which primary production peaks (Meeuwis and Lutjeharms 1990). Potentially, the energetic costs associated with reproductive organ/tissue development may be mitigated by coinciding with the period of highest prey availability (Jönsson 1997).

In conclusion, *D. c. hottentotus* in southern Angola is a generalist carnivore that feeds on a variety of benthic invertebrates and has a very similar diet to that recorded in South African conspecifics. Species belonging to the *D. cervinus* complex are able to feed on a range of prey items and local dietary composition is probably driven by the abundance of prey. In southern Angola, seasonal shifts in prey diversity are probably attributed to the influence of the nutrient-rich Benguela Current on the benthic invertebrate communities, whereas non-significant differences in feeding intensity could be attributed to energetic requirements during the extended spawning season.

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