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ORIGINAL PAPER

Nursery provision of red-algal habitats in temperate Algoa Bay, South Africa

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Abstract

This study examines the importance of both macroalgal heterogeneity and specific macroalgal species or morphotypes to nursery provision for juvenile sparids (*Diplodus capensis* and *Sarpa salpa*) in a shallow (< 2 m), sheltered rocky cove in warm-temperate Algoa Bay, South Africa. The rocky cove is comprised of a mosaic of two main benthic habitats; canopy-forming *Plocamium corallorhiza* beds on rocky outcrops and flat reef dominated by low growing red algae morphotypes. We assessed macroalgal communities and the trophic ecology (stomach contents and isotopes), abundance and size structure of *D. capensis* and *S. salpa* in the two different benthic habitats and the resources/food associated with the dominant macroalgae species/morphotypes. We found high densities of *S. salpa* and *D. capensis*, in both high profile reef (rocky outcrops) and low profile (flat) reef. Within this habitat mosaic resources (epiphytes and macroinvertebrates) were more abundant in the non-canopy forming low growing macroalgae (*Laurencia* spp. and coralline turf algae) and these algae were also assimilated in the diets of both sparids. The high abundance of both juvenile *S. salpa* and *D. capensis* in high profile and low profile reef, suggests that within this mosaic of habitats these species may be using canopy-forming algae in the high profile reef for shelter and non-canopy forming algae in both the high and low profile reef for food. This shows that macroalgal habitats comprising several morphotypes have the potential to support higher juvenile diversity and abundance through both food provision and shelter.

Keywords Plocamium · Laurencia · Habitat · Resources · Sparids · Trophic ecology

Introduction

One of the most critical ecosystem functions provided by shallow coastal habitats is as nurseries for the juveniles of marine fish, many of which are targeted in fisheries as larger individuals. Core nursery areas (juvenile abundance hotspots) within nursery seascapes are typically areas that are structurally complex, have high food availability, and provide shelter to juveniles (from predation and environmental pressures, such as temperature extremes and strong tidal currents) (e.g. Heck and Crowder 1991; Beck et al. 2001). The provision of structure for both food and refuge in vegetated coastal habitats (such as mangroves, seagrass and macroalgae) results in elevated density, growth and survival of juvenile fish (Beck et al. 2001; Heck et al. 2003; Hyndes et al. 2003) making these habitats important core nursery areas within a habitat mosaic or nursery seascape (Nagelkerken et al. 2015).

Many of the studies that have assessed the nursery function of vegetated coastal habitats have focussed on seagrass

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and as such, seagrass is often considered the most important core nursery habitat for juvenile fishes (Lefcheck et al. 2019). Although considerably less work has focussed on the nursery provision of macroalgae within nursery seascapes, James and Whitfield (2023) reviewed the nursery provision of macroalgae and showed that the nursery provision of small canopy-forming brown algae from the Fucalean genera (*Sargassum* spp. and *Cystoseira* spp.) may be comparable with that of seagrass. Recently we compared abundance of juvenile fish and the structural complexity of sub-littoral eelgrass (*Zostera capensis*) in estuaries and canopy-forming red algae *Plocamium corallorhiza* beds in a shallow (< 2 m), sheltered rocky cove in temperate Algoa Bay, South Africa. The structural complexity and nursery function of these two macrophytes was found to be comparable (Mkhize et al. 2024).

The nursery function of canopy-forming *P. corallorhiza* beds was inferred based on the occurrence of large numbers of juvenile sparids in *P. corallorhiza* beds and high structural complexity (1303 individuals/m^2; 17 cm canopy height and 1.8 fractal dimension) potentially providing protection from predation (Mkhize et al. 2024). High nursery value is also conferred through sufficient food supply (Hinz et al. 2019) but this was not tested. Furthermore, littoral rocky reefs may have a variety of different algal species and morphotypes (defined in Hinz et al. (2023) as structurally similar species) and this is true of Algoa Bay, where although *P. corallorhiza* is the dominant canopy-forming algae in shallow water (1–3 m) other algal species are dominant depending on exposure (water movement), rugosity, depth and substrate (Knoop 1988; Moriarty 2019). For example, on the wave-exposed coastline where reef is comprised of jutted rocks with gullies and pools, coralline turf cover is higher in areas with greater sand cover, while cover of foliose algae (such as *Laurencia flexuosa*, *L. natalensis*, *Dictyota dichotoma* and *Calliplepharis fimbriata*) and *P. corallorhiza* is greater in deeper water with more boulder or rock substrate cover (Moriarty 2019).

Macroalgal heterogeneity (patchiness and variety of functional forms) plays an important role in nursery provision in coastal seascapes, with macroalgal habitats comprising several functional forms (a mixture of canopy and understory taxa) having the potential to support higher juvenile diversity and abundance rather than a single homogeneous habitat type covering the same area; with this linked to both shelter (protection from predation) and food provision (James and Whitfield 2023). In temperate Mediterranean littoral rocky reefs, structurally complex *Cystoseira* forests, which have both canopy and understory taxa present, have more invertebrate prey than low growing algal turf and a threefold greater abundance of juvenile fishes (related to food provision) (Cheminée et al. 2017). Similarly, Hinz et al. (2019) found that structurally complex canopy-forming algae (such as *Cystoseira* spp. and *Halopteris* spp.) have more invertebrate prey than simpler algal morphotypes (such as *Dictotales* spp.). Along the northeast coast of Brazil, Feitosa and Ferreira (2014) found that although food resources were available in both calcareous algal turf and high canopy *Sargassum*, higher densities of small juvenile parrotfishes were associated with *Sargassum* (related to shelter).

The importance of both macroalgal heterogeneity and specific macroalgal species or morphotypes to different fish species is still, however, poorly understood (Hinz et al. 2023). The rocky cove in Algoa Bay is comprised of a mosaic of two main benthic habitats; *P. corallorhiza* beds on rocky outcrops and flat reef dominated by low growing algae morphotypes. In this study we focussed on the importance of different algae species and morphotypes in nursery provision (food and shelter) for juvenile sparids within the cove. We assessed macroalgal communities and the trophic ecology, abundance and size structure of dominant juvenile sparids in the two different benthic habitats and the resources/food associated with the dominant macroalgae species/morphotypes. This forms part of a larger research programme on shallow water nursery habitats in Algoa Bay.

Methods and materials

Study species

This study focussed on two sparid species *Diplodus capensis* and *Sarpa salpa*, which are abundant as young-of-the-year recruits in both eelgrass *Zostera capensis* beds in estuaries and *Plocamium corallorhiza* beds on shallow littoral rocky reefs in Algoa Bay (Mkhize et al. 2024). *Diplodus capensis* is endemic to southern Africa, occurring from Cape Point to southern Mozambique, while *S. salpa* occurs from the Mediterranean and parts of the eastern Atlantic and along the South African coastline to southern Mozambique (Mann 2013). Both *D. capensis* and *S. salpa* recruit into the rocky intertidal littoral zone from 9 mm SL and migrate to sublittoral nursery habitat from approximately 90 mm SL (Christensen 1978). Sub-adults and adults are found in slightly deeper subtidal reef (Mann 2013). Juvenile *D. capensis* are omnivorous, with Christensen (1978) finding that the diet of juveniles of all size classes (5–165 mm SL) were composed mainly of animals (copepods, isopods, amphipods, polychaetes and ostracods), with a small algal component. Juvenile *S. salpa* are primarily herbivorous, with the importance of animals (copepods) in the diet decreasing substantially with size (from 25 mm SL), such that by > 75 mm SL individuals feed primarily on algae (Rhodophytes and Chlorophytes) (Christensen 1978).

Study site

Algoa Bay is a large temperate embayment situated on the southern coastline of South Africa between two headlands; Cape Recife in the west and Cape Padrone in the east. Most of the shoreline of Algoa Bay is comprised of sandy beaches (74 km), particularly in the eastern sector, with the western sector comprised of modified shoreline (dollose and harbour walls – 14 km) and rocky shores (9 km), with the 6 km stretch of coast from Cape Recife comprising a calcareous sandstone rock platform. Two predominantly open estuaries enter the western half of the bay, the Swartkops and Sundays estuaries, with *Zostera capensis* seagrass (53.6 ha) found in the lower reaches of the Swartkops Estuary (Fig. 1a).

The shallow subtidal cove (1.8 ha) known as Flat Rocks is located off the eastern shore of Cape Recife. Flat Rocks is the only cove within the calcareous sandstone rock platform (Fig. 1b), with an average depth of ~1.5 m during spring low tides. Semi-diurnal tides occur in the study area with a mean range of between 1.6 m (springs) and 0.5 m (neaps). The study area is sheltered in the lee of Cape Recife and is protected from severe wave action as most waves approach from the south and south-west. Sea water temperatures range from 12 to 27 °C (Beckley 1985). Two main benthic habitats are present at Flat Rocks; rocky outcrops with high rugosity (mean rugosity index = 1.3) hereafter called high profile reef and flat reef with low rugosity (mean rugosity index = 1.1) hereafter called low profile reef with small sand patches (Fig. 1c).

Littoral habitats with a depth of 1 to 1.5 m were sampled from February to June 2021, during the period following peak recruitment of sparids into nursery habitats (Christensen 1978; Whitfield 2019).

Macroalgae census

Samples of different macroalgae species occurring on low profile reef and high profile reef were collected by snorkelling throughout the cove and were identified *ex situ* in the laboratory to the nearest taxonomic level as reference for image analysis. Images were then taken 1 m above the different littoral habitat patches in 0.5 × 0.5 m photo-quadrats (10 quadrats per habitat spaced at least 1 m apart) along a similar depth gradient (1–1.5 m – see Fig. 1c). The percentage live cover for each macroalgae species/genus/morphotype present in the photo-quadrats was visually estimated following Hill and Wilkinson (2004).

Fish census

Fish associated with the two different habitats were surveyed using stereo remote underwater video (sRUV) systems developed to measure small-bodied fish and juveniles. The sRUV systems have two GoPro Hero Black 7 cameras, with cameras placed straight on the same plane at a separation of 200 mm between lenses and an inward angle of two degrees (Mkhize et al. 2024). The sRUVs were deployed 20 min before low tide and left to record for 60 min before retrieval between March and November 2021. The sRUVs were deployed randomly in different areas of low and high profile reef each sampling occasion (Fig. 1c) and were positioned to point at the dominant macroalgal species/genus/morphotype in each site (i.e. *P. corallorhiza* in high profile reef). Deployments were made in high profile reef and low profile reef for a total of twelve deployments (720 min) in high profile reef and nine deployments (540 min) in low profile reef.

Videos were analysed using EventMeasure (www.seagis.com.au). Relative abundance of a species was measured at MaxN; where MaxN is the maximum number of a particular species measured in a single image (Seager 2008). At MaxN, individuals were identified to the lowest taxonomic level possible. The size of individuals present at MaxN were measured at fork length (mm FL) using EventMeasure, only individuals that were observed in both cameras, of the stereo-pair, were measured. Measured individuals were assigned to life stages (young-of-the-year juveniles, larger juveniles and adults) using published growth parameters (Mann 2013).

Algal associated epiphytes and prey

The invertebrates and epiphytes associated with the dominant macroalgae present at Flat Rocks were collected within a 20 × 20 cm quadrat. On each sampling occasion samples of *Laurencia* spp. (*Laurencia glomerata*, *L. flexuosa* and *L. natalensis*, hereafter called *Laurencia*) were collected from three randomly placed quadrats within low profile reef (Fig. 1c). Three replicate samples of *P. corallorhiza* were collected in the same way from high profile reef. *Laurencia* and *P. corallorhiza* specimens were cut at the base of the thallus (Chen et al. 2020). Coralline turf was collected as above using a paint scraper from the lower intertidal (Fig. 1c). These were immediately placed on ice for storage. Sampling took place on three sampling occasions on a spring low tide in February, March and April 2021.

Invertebrate sampling followed that of Mudroch and MacKnight (1994) and Fraser et al. (2020). Briefly, a Van Veen grab was used to collect sediment adjacent to the submerged macroalgae beds in the sand patches (30 cm^2 per grab x 3 replicate grabs per sample). Sediment was then swirled in a bucket and rinsed into a conical mesh sieve ensuring all invertebrates were collected. Samples were

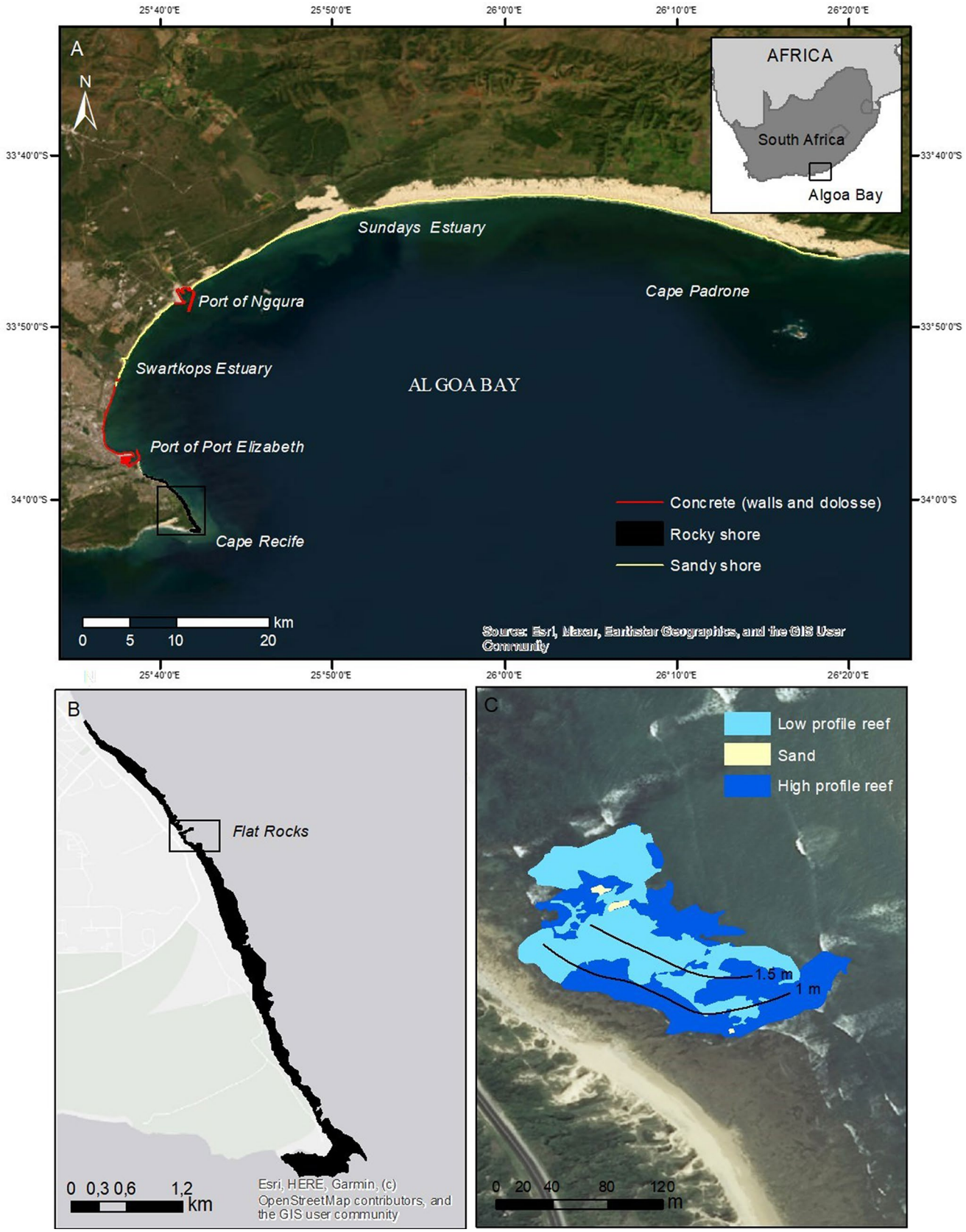


Fig. 1 Study area showing (**A**) the location of rocky, sandy and modified shoreline in Algoa Bay (**B**) the study site Flat Rocks and (**C**) the two main macroalgal habitats; high profile reef and low profile reef interspersed with sand patches. The depth transect and location of the sandy patches sampled are shown

placed on ice for storage. Three replicates per sampling trip were conducted.

Chlorophyll-*a* as a proxy for epiphyte biomass was quantified according to Dodds (1991). Samples were soaked in 500 ml beakers containing water. The samples were then sonicated for two minutes to remove suspended epiphytes. After removal of the macroalgae, samples were then vacuum filtered through a 500 µm GF/F filter and then placed in a test tube with 8 ml 90% acetone for 48 h in a refrigerator to extract chlorophyll-*a* and phaeopigments concentrations using a Turner 10-AU fluorometer. Total epiphyte chlorophyll was converted to mg.m^{-2} following Pinto et al. (2001). Macroalgae were also inspected under a light microscope to confirm epiphyte removal post sonication. Remaining macroalgae and invertebrates were placed into a 500 ml sample jar and preserved in a solution of 5% formalin containing phloxin-B (Kalejta and Hockey 1991; Kendrick and Lavery 2001) and stored in a cool, dark storage room until analysis. Epiphytic biomass was compared between macroalgal types using a one-way ANOVA and post-hoc Tukey tests.

All the invertebrates in each sample were identified to the lowest taxonomic resolution possible using available reference guides (Milne and Griffiths 2013; Branch et al. 2017) and the abundance (number of individuals.m^{-2}) and biomass (dry weight - mg.m^{-2}) of the major invertebrate taxa present calculated for each of the dominant macroalgal species/morphotypes and the sediment. To compare the differences in invertebrate resources between the dominant macroalgal species/morphotypes and sediment, a one-way ANOVA and post-hoc Tukey tests were used.

Gut content and stable isotope analysis of *Diplodus capensis* and *Sarpa salpa*

A total of 31 young-of-the-year (YOY) *Diplodus capensis* individuals (43–68 mm FL) and 29 YOY *S. salpa* individuals (54–80 mm FL) were captured at Flat Rocks in high and low profile reef in shallow water (< 1.5 m depth) using hand-operated lobster traps. Individuals captured for the purpose of the study were anaesthetised using clove oil (as per Iversen et al. 2003) and euthanized by placing them on ice for 30 min. In the laboratory they were immediately weighed, measured, and then frozen (-20 °C).

In the laboratory, the contents of each specimen's stomach were emptied and visually investigated using a dissecting microscope at a magnification of between 10 x and 40 x. The presence-absence and proportions of different food resources present in each gut were noted to the lowest taxonomic resolution possible (Hyslop 1980). Food items were then expressed as a percentage of the total volume of stomach contents (%V) and the percentage frequency of occurrence (%F), which is the percent of stomachs containing a specific food item (Hyslop 1980).

The dietary composition of *D. capensis* and *S. salpa* was investigated through the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic ratios in the fish species and the food resources that they potentially forage on. Material collected (as above) for isotope analysis included epiphytes, epibionts, benthic invertebrates and macroalgae and dorsal muscle tissue from individuals of *D. capensis* and *S. salpa.* Samples were prepared following standard preparation procedures, as in Rishworth et al. (2018). Isotopic analyses were conducted at the UP Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria (Pretoria, South Africa) by combusting samples at 1200 °C using a Flash EA 1112 Series elemental analyser which was connected to a Delta V Plus stable light isotope ratio mass spectrometer through a ConFlo IV system (equipment supplied by Thermo Fischer, Bremen, Germany). This provided the relative carbon (^{13}C and ^{12}C) and nitrogen (^{15}N and ^{14}N) ratios. All SI data were presented as the fractional difference between the samples and known international standard values (‰), these being Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric N_2 ($\delta^{15}N$):

$$\delta X(‰) = [(R_{sample}\text{-}R_{standard})/R_{standard}\text{-}1]$$

where X is $\delta^{13}C$ or $\delta^{15}N$ and R is the ^{13}C:^{12} or ^{15} N:^{14}N ratio. Between every 11 samples, a blank sample was run to correct spectrometric SIA values against the laboratory running standards. Stable isotope analysis was conducted using the "SIMMR" R package (Parnell and Inger 2019).

Results

Macroalgal composition

A total of 10 macroalgae species/morphotypes were identified from the high profile reef photo-quadrats and six from the low profile reef photo-quadrats. Red algae (Rhodophyta) were the dominant phyla in both reef profiles (Fig. 2). Both the high and low profile reef had a high cover of algae, with 99% algal cover on the high profile reef and 88% on the low profile reef. *Plocamium corallorhiza* (33 ± 4%) was the dominant algal species on the high profile reef, followed by coralline turf (25 ± 4%), *Laurencia glomerata* (17 ± 6%) and *L. flexuosa* (6 ± 1%) (Fig. 2). Although we were not able to identify the coralline turf algae to species level from the photos, the coralline turf was mainly comprised of *Jania* spp. and *Arthrocardia* spp. (Table S1). Low profile reefs were dominated by low-growing *L. glomerata* (42 ± 2%), coralline turf (39 ± 2%) and upright coralline algae (4 ± 1%), with 12 ± 2% sand cover (Fig. 2).

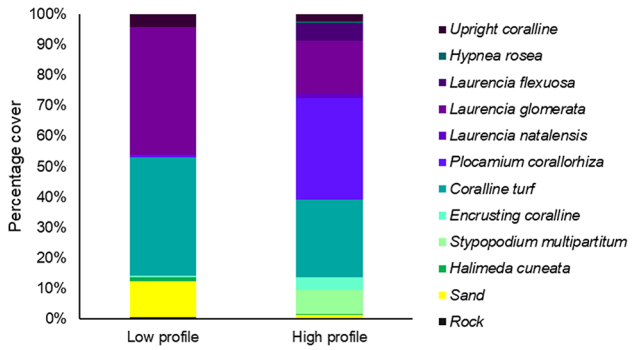


Fig. 2 Percentage cover of macroalgae, sand and rock on low and high profile reef

Table 1 Mean relative abundance - MaxN (mean ± SE) and percentage contribution of fish species recorded on low profile and high profile reef at flat rocks, Algoa Bay

Taxon	Low profile		High profile	
	MaxN (SE)	%	MaxN (SE)	%
Sparidae				
Sarpa salpa	**13.9 (7.9)**	**29.8**	**18.3 (3.5)**	**41.0**
Diplodus capensis	**19.8 (5.0)**	**42.4**	**12.9 (2.5)**	**28.9**
Diplodus hottentotus	2.4 (0.8)	5.2	2.0 (0.5)	4.5
Boopsoidea inornata	2.1 (0.9)	4.5	2.3 (0.6)	5.0
Sparodon durbanensis			1.4 (1.4)	3.2
Gymnocrotaphus curvidens	0.3 (0.2)	0.7	0.1 (0.1)	0.2
Spondyliosoma emarginatum	0.2 (0.2)	0.5		
Haemulidae				
Pomadasys olivaceus	6.0 (3.2)	12.9	4.2 (2.9)	9.3
Latridae				
Chirodactylus brachydactylus	1.0 (0.3)	2.1	1.1 (0.3)	2.4
Clinidae				
Clinus superciliosus	0.6 (0.2)	1.2	0.3 (0.1)	0.7
Labridae				
Thalassoma amblycephalum	0.4 (0.4)	1.0		
Mugilidae				
Mugilid spp.	0.4 (0.3)	1.0	2.0 (0.9)	4.5
Carangidae				
Uraspis secunda	0.3 (0.2)	0.7		
Myliobatidae				
Myliobatis aquila	0.1	0.2		
Serranidae				
Epinephelus marginatus			0.1 (0.1)	0.2
Tetraodontidae				
Geneion honckenii			0.1 (0.1)	0.2
Total MaxN	46.7 (6.8)		44.8 (5.3)	
Total species	13		13	

Fish assemblages and different algal habitats

A total of 18 fish species were recorded, with 13 species on low profile reef and 13 on high profile reef. *Diplodus capensis* (42%) followed by *Sarpa salpa* (30%) dominated the fish assemblage on low profile reef, while *Sarpa salpa* (41%) followed by *Diplodus capensis* (29%) were the most abundant fish species on high profile reef (Table 1). Although not significant, the abundance of *S. salpa* was highest on high profile reef (18.3 ± 3.5) compared with low profile reef (13.9 ± 7.9), while the abundance of *D. capensis* was higher on low profile reef (19.8 ± 5) than high profile reef (12.9 ± 2.5) (Fig. 3).

The measured individuals of *S. salpa* and *D. capensis* on the two macroalgal habitats (low and high profile reef) were all juveniles and predominantly young-of-the year (YOY) recruits, with the smallest *S. salpa* (37 mm FL) measured in *P. corallorhiza* beds on high profile reef. *Diplodus capensis* were predominantly YOY recruits (20–120 mm FL) in both habitats.

Feeding ecology

Young-of-the-year *S. salpa* were predominantly herbivorous (Table 2). Epiphytes dominated the diet of *S. salpa* in the smallest 50–59 mm FL size class (43.31%V; 100%F), and decreased in importance in the larger 60–69 and 70–79 mm FL size classes (23.1–27.1%V; 100%F). In these larger size classes *Laurencia* dominated the diet (50.4–55.4%V; 100%F). Coralline turf (7.5–13.9%V; 41.7–75%F) and *P. corallorhiza* (3.1–5.6%V; 25-33.3%F) were also important in all size classes, with invertebrates (amphipods and polychaetes) comprising a smaller component of the diet. Amphipods were the dominant invertebrate in the smallest 50–59 mm FL size class (3.3%V; 11.1%F) but were absent in the diet of the larger size classes. Polychaetes were absent in the stomachs of the smallest size class and the dominant invertebrate in the stomachs of the larger 60–69 and 70–79 mm size classes (5.4–10%V; 50-58.3%F).

Young-of-the-year *D. capensis* were omnivorous. Epiphytes (mostly diatoms) dominated the diet of *D. capensis* in all size classes (34.7–41.4%V; 71.4–88.9%F), followed by unidentified macroalgae (15-27.9%V; 71.4–100%F), unidentified invertebrates (6.7–25%V; 44.4–85.7%F) and polychaetes (7.2–11%V; 44.4–80%F). Amphipods were important in the diet of the 40–49 mm FL (5%V; 22.2%F) and 50–59 mm FL (4.3%V; 26.7%F) size classes but not in the largest 60–69 mm FL size class (0.7%V; 14.3%F). Coralline turf, *Laurencia* and *P. corallorhiza* were found in small quantities and not in all size classes (Table 3).

The highest $\delta^{13}C$ (-11.56) and $\delta^{15}N$ (15.62) was identified in *D. capensis* YOY juveniles, while the lowest $\delta^{13}C$ (-16.69) and $\delta^{15}N$ (12.86) belonged to *S. salpa* YOY juveniles (Fig. 4). Mean $\delta^{13}C$ was lower in the *S. salpa* juveniles (-15.53 ± 0.55) compared to the *D. capensis* juveniles (-13.71 ± 1.23), and mean $\delta^{15}N$ was lower in the *S. salpa* juveniles (13.41 ± 0.25) compared to the *D. capensis* juveniles (14.98 ± 0.44). Mean $\delta^{13}C$ for the prey

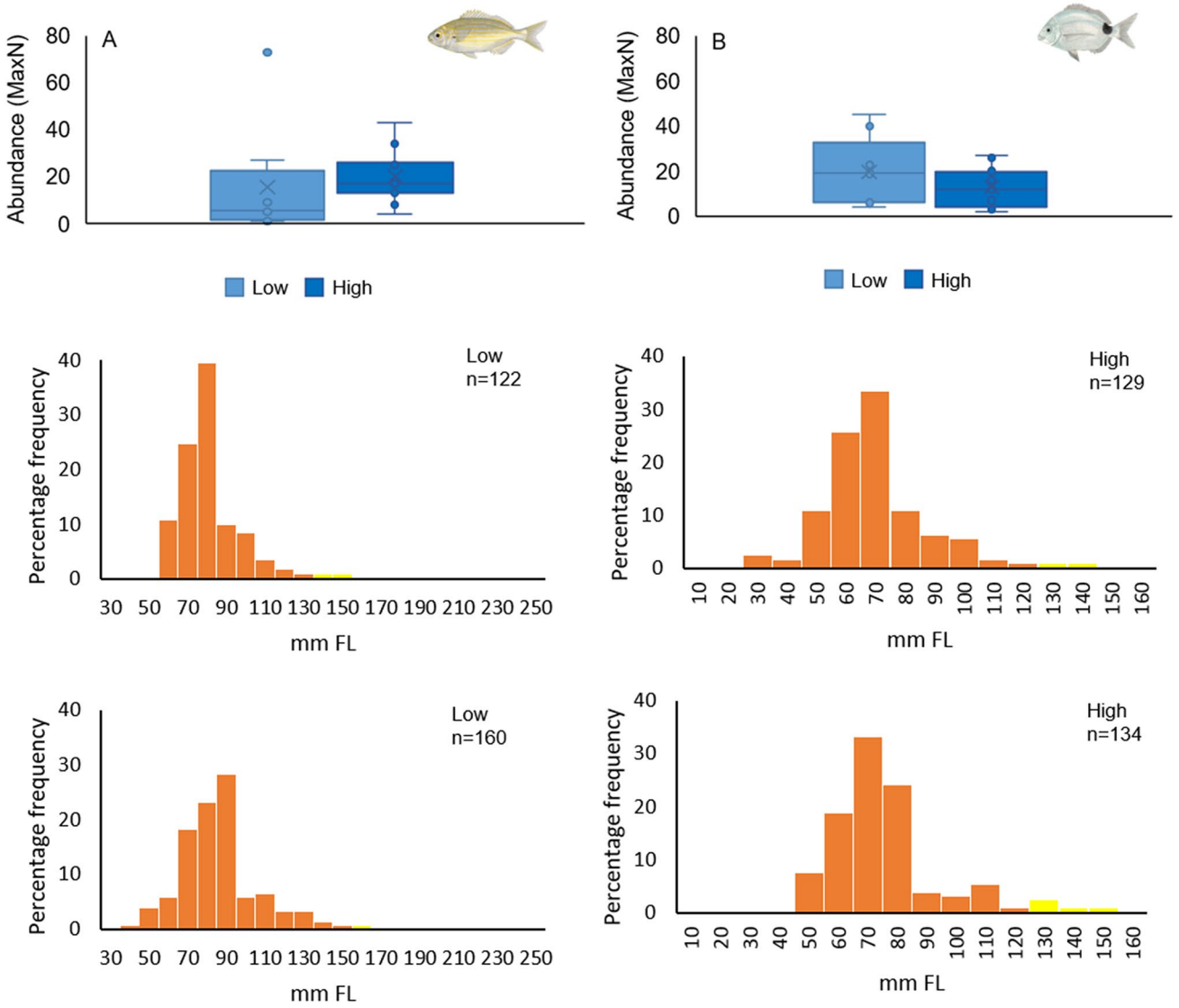


Fig. 3 Box plots showing abundance and length frequency histograms of (**A**) *Sarpa salpa* and (**B**) *Diplodus capensis*. Length frequency histogram bars: orange = young-of-the-year (YOY), yellow = larger juveniles

Table 2 The relative importance of different taxa found in the stomach contents of *Sarpa salpa* ($n = 29$) caught at flat rocks between February and April 2021. %V (mean ± SE) = percentage volume, %F = percentage frequency of occurrence

Dietary category	50–59 mm FL ($n = 9$)		60–69 mm FL ($n = 12$)		70–79 mm FL ($n = 8$)	
	%V	%F	%V	%F	%V	%F
Invertebrates						
Amphipod	3.3 (3.3)	11.1	0	0	0	0
Polychaete	0	0	5.4 (2.1)	58.3	10 (5.1)	50
Isopod	0	0	0	0	0	0
Unidentifiable invertebrate	1.1 (0.7)	22.2	3.8 (2.5)	33.3	1.3 (0.8)	25
Algae						
Epiphyte	43.3 (5.7)	100	27.1 (5.8)	100	23.1 (3.3)	100
Laurencia	28.9 (6.8)	88.9	50.4 (6.6)	100	55 (4.5)	100
Plocamium corallorhiza	5.6 (2.9)	33.3	5.4 (3.4)	33.3	3.1 (2.5)	25
Coralline turf	13.9 (6.2)	44.4	7.5 (3)	41.7	7.5 (2.5)	75
Unidentifiable macroalgae	3.9 (2.6)	22.2	1.3 (0.9)	16.7	0	0

Table 3 The relative importance of different taxa found in the stomach contents of *Diplodus capensis* caught at flat rocks between February and April 2021. %V (mean ± SE) = percentage volume, %F = percentage frequency of occurrence

Dietary category	40–49 mm FL ($n=9$)		50–59 mm FL ($n=15$)		60–69 mm FL ($n=7$)	
	%V	%F	%V	%F	%V	%F
Invertebrates						
Amphipods	5 (4.4)	22.2	4.3 (2.7)	26.7	0.7 (0.7)	14.3
Polychaete	7.2 (3.4)	44.4	11 (2.5)	80	9.3 (3)	71.4
Isopod	0	0	3 (1.4)	33.3	0	0
Unidentifiable invertebrates	6.7 (3.2)	44.4	24.3 (5.9)	73.3	25 (5.3)	85.7
Algae						
Epiphytes	41.1 (8.4)	88.9	34.7 (6)	86.7	36.4 (11.2)	71.4
Laurencia	0	0	2.7 (2.7)	6.7	0	0
Plocamium corallorhiza	0	0	0	0	0.7 (0.7)	14.3
Coralline turf	0	0	2.7 (2.7)	6.7	0	0
Unidentifiable macroalgae	15 (2.2)	100	15.3 (4.4)	80	27.9 (9.3)	71.4

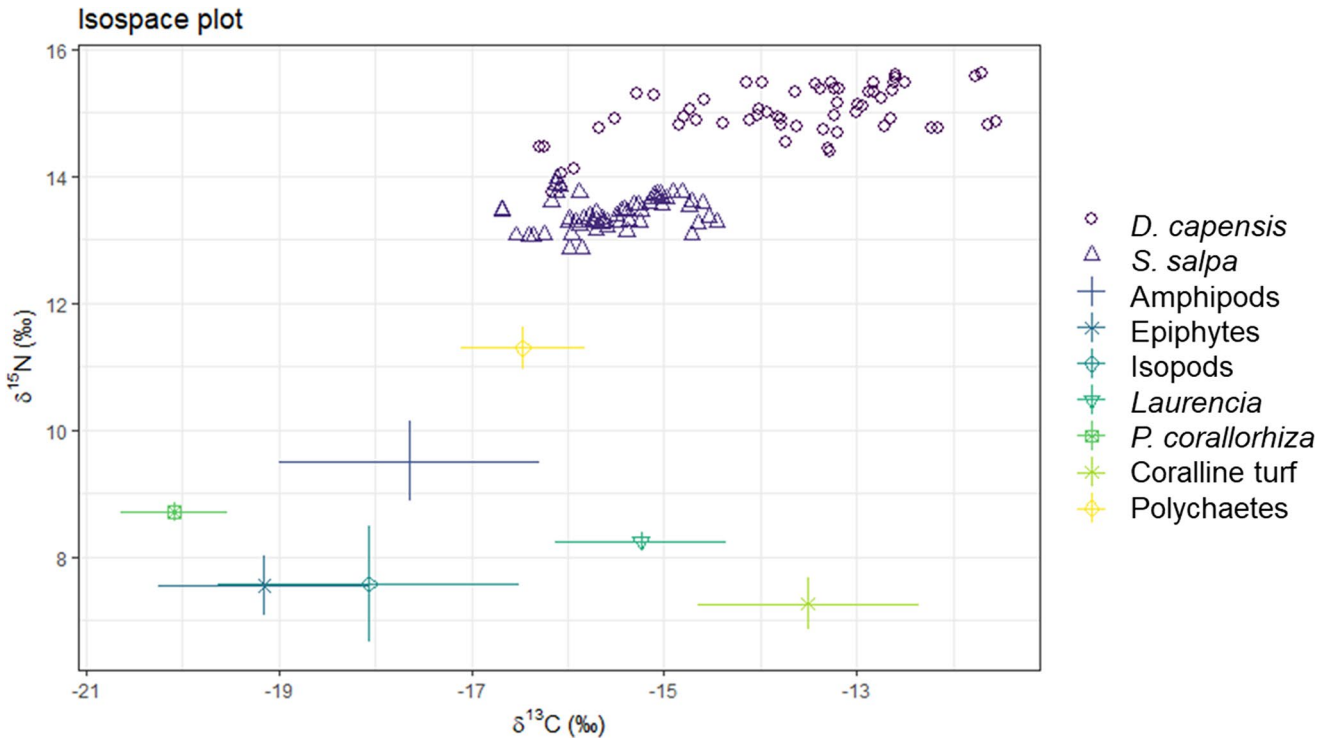


Fig. 4 Stable isotope isospace plot showing $\delta^{13}C$ and $\delta^{15}N$ ratios for the consumers (*D. capensis* and *S. salpa*) and their food resources (amphipods, isopods, polychaetes, epiphytes, *P. corallorhiza*, *Laurencia*, coralline turf)

resources were as follows: amphipods (-17.64 ± 1.35), epiphytes (-19.15 ± 1.1), isopods (-18.07 ± 1.57), *Laurencia* (-15.24 ± 0.89), *P. corallorhiza* (-20.09 ± 0.55), coralline turf (-13.51 ± 1.15) and polychaetes (-16.47 ± 0.65). Mean $\delta^{15}N$ for the prey resources were as follows: amphipods (9.51 ± 0.63), epiphytes (7.54 ± 0.46), isopods (7.57 ± 0.92), *Laurencia* (8.25 ± 0.14), *P. corallorhiza* (8.71 ± 0.14), coralline turf (7.26 ± 0.41) and polychaetes (11.3 ± 0.33). *Diplodus capensis* and *S. salpa* had greater $\delta^{15}N$ than all prey resources and had greater $\delta^{13}C$ than all prey resources except for coralline turf, *Laurencia* and polychaetes in some individuals. The isotopic ratios for *D. capensis* indicate a wider trophic niche compared to *S. salpa*, with *D. capensis* possibly foraging at a higher trophic level compared to *S. salpa*, with overlap in the $\delta^{13}C$ for *D. capensis* with polychaetes, coralline turf and *Laurencia*. In contrast the $\delta^{13}C$ for *S. salpa* only overlapped with *Laurencia* and polychaetes (Fig. 4).

Algal associated epiphytes and prey

The mean epiphytic chlorophyll biomass was significantly different between algal types (ANOVA, F (2, 24) = 3.70, $P = 0.02$) and significantly higher (Tukey's HSD test, $P = 0.013$) in the coralline turf (47.6 ± 10.4 mg.m^{-2}) samples compared to *P. corallorhiza* (20.2 ± 3.6 mg.m^{-2}) samples (Fig. 5a). Similarly, the abundance of invertebrate prey was significantly different between algal types (ANOVA, F (3, 32) = 32.7, $P = 0.02$) and significantly more abundant in all algal types than in sediment (Tukey's HSD test, $P < 0.001$) and significantly more abundant in the coralline turf (7850 ± 536 per m^2) samples compared to *Laurencia* (13909 ± 1855 per m^2, $n = 9$) samples and in *Laurencia* compared to *P. corallorhiza* (4639 ± 793 per m^2) samples (Tukey's HSD test, $P < 0.05$) (Fig. 5b).

Invertebrate prey biomass differed significantly between algal types (ANOVA, F (3, 32) = 7.66, $P = 0.0006$), with invertebrate biomass significantly higher (Tukey's HSD test, $P < 0.05$) within the *Laurencia* (1791 ± 347 mg.m^{-2}) and coralline turf (1795 ± 231 mg.m^{-2}) samples compared to sediment (516 ± 92 mg.m^{-2}) (Fig. 5c).

Discussion

Juvenile fish are thought to actively use/select habitat within nursery seascapes based on food availability and predation risk (Jordan et al. 1996; Laegdsgaard and Johnson 2001), with high quality nurseries providing both shelter and food for juveniles (Hinz et al. 2019). In our study we found high densities of young-of-the-year sparids, particularly *Sarpa salpa* and *Diplodus capensis*, in both high profile reef (rocky outcrops) and low profile (flat) reef. Within this habitat mosaic resources (epiphytes and macroinvertebrates) were more abundant in the low growing macroalgae (*Laurencia* and turf algae) and these algae were also assimilated in the diets of *S. salpa* and *D. capensis*. The high abundance of both *S. salpa* and *D. capensis* on high profile and low profile reef, suggests that within this mosaic of habitats these species may be using canopy-forming *Plocamium corallorhiza* on the high profile reef for shelter and low growing algae on both the high and low profile reef for food.

Juvenile sparids dominated the fish assemblage throughout the cove (low and high profile reef). South Africa is the global biodiversity hotspot for sparids, with 42 species

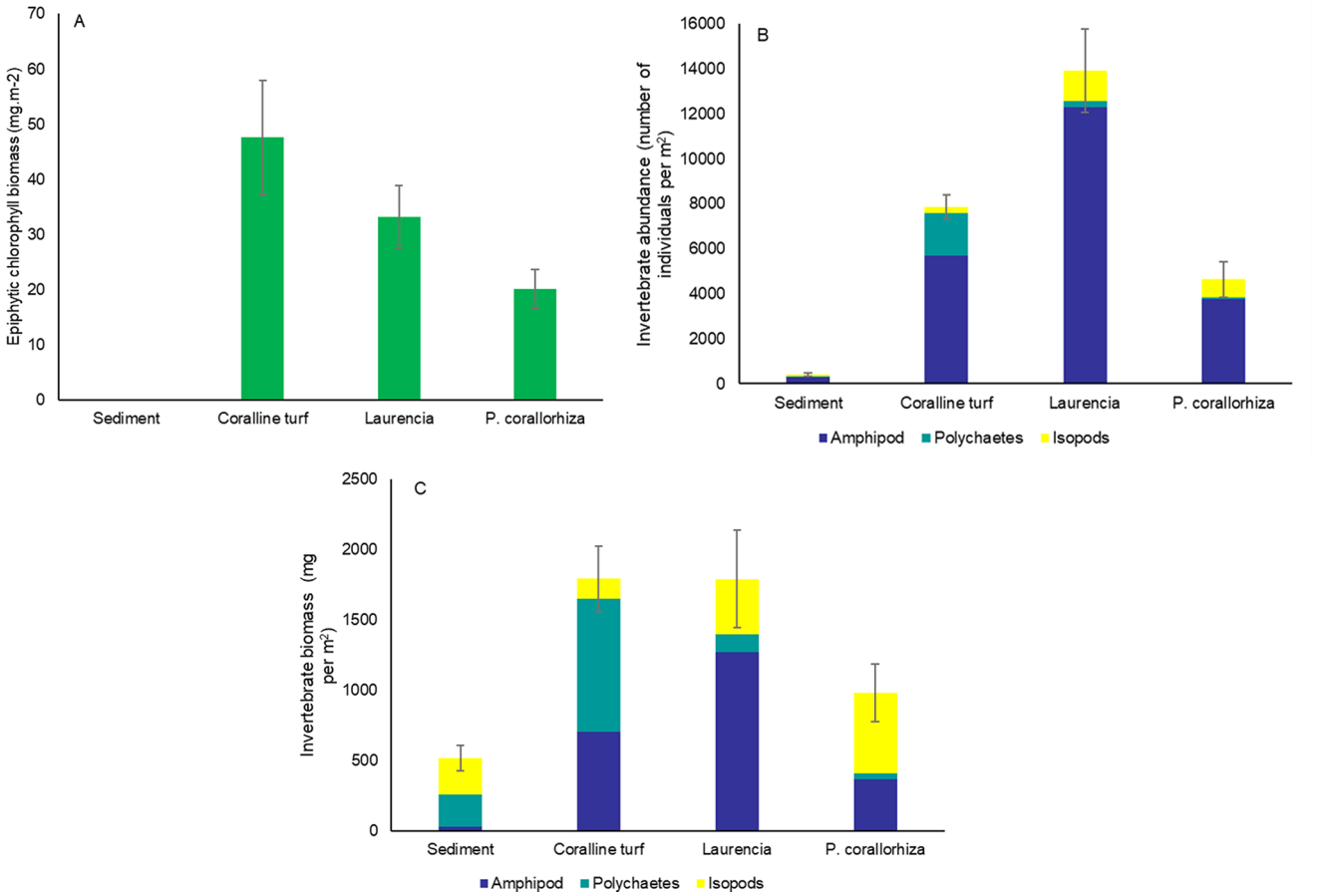


Fig. 5 Mean (±SE) (**A**) epiphytic chlorophyll biomass (mg.m^{-2}), (**B**) abundance (number of individuals.m^{-2}) of invertebrates and (**C**) biomass (mg. m^2) of invertebrates associated with each of the sampled macroalgal species/genus/morphotype

recorded (Whitfield and Mann 2023). The dominance of this family in the inshore coastal environment is reflected in the shore-based fishery, with 11 of the 21 of the teleosts caught on rocky shores along the South African south coast being sparids (Britz et al. 2001). Juvenile habitats for four (*D. capensis*, *S. salpa*, *Diplodus hottentotus* and *Rhabdosargus holubi*) of the seven sparids recorded in this study are located in shallow intertidal and sub-littoral waters in both estuaries and rocky shores, with adult habitat being deeper subtidal reef (Mann 2013; Watt-Pringle et al. 2013; Mkhize et al. 2024).

Although recently recruited (young-of-the-year) sparids were abundant on low and high profile reef, the herbivorous *S. salpa* dominated the fish assemblage in the high profile reef and the omnivorous *D. capensis* on the low profile reef. The high abundance and dominance of *S. salpa* on high profile reef may be related to both high cover of canopy-forming *P. corallorhiza* as well as the variety of algal food resources available. In South Africa, rocky shores with high cover of canopy-forming macroalgae, such as kelp beds (brown algae), are given as the principal habitat for this species (Gerking 1984), although they feed primarily on understory red and green algae (Joubert and Hannekom 1980). Juvenile *S. salpa* are also recorded in high numbers in the lower reaches of predominantly open estuaries with extensive seagrass beds (James and Harrison 2010a&2010b), where they feed on filamentous algae and seagrass (Bennett 1989).

Ten macroalgae species/morphotypes were found to occur on high profile reef and six on low profile reef, with red algae dominating throughout. *Plocamium corallorhiza* was found predominantly on high profile reef, with *Laurencia* spp. (foliose algae) and coralline algal turf dominating the algal cover on low profile reef patches. The cove at Flat Rocks, is fairly deep (+ 1.5 m) and with a rocky substrate and high cover of canopy-forming *P. corallorhiza*, is atypical of the rocky shoreline east of Cape Recife, which has a gentle slope (< 1 m in the sub-littoral zone) consisting of pebbles and boulders, with sand between the rocks and very few deep pools (McLachlan et al. 1981). Typically, foliose algae (including *Laurencia* spp.) and *P. corallorhiza* are associated with boulder/rock substrates in deeper (1–3 m) water, with coralline turf having a higher abundance in shallower depths (< 1 m) and sandy substrates (Moriarty 2020).

Young-of-the-year *S. salpa* (54–80 mm FL) at Flat Rocks are primarily herbivorous, with the contribution of animals in the diet ranging from only 4% (%V) in the smallest 50–59 mm FL size class to 11% in the largest 70–79 mm FL size class. In our study although epiphytes that were primarily diatoms and *Laurencia* were the dominant algae consumed, juveniles were also consuming *P. corallorhiza* and turf algae but in smaller quantities. The low consumption of *P. corallorhiza* may be linked to both the low biomass of epiphytes and palatability of this species. Another member of the *Plocamium* genus, *P. brasiliense* produces secondary metabolites to prevent herbivore action and biofouling (Vasconcelos et al. 2010), and this may be similar in *P. corallorhiza*. By producing chemical defences against herbivory canopy-forming algae are then available for shelter for herbivorous fishes. For example, in the Mediterranean shallow sublittoral *Cystoseira* forests co-exist with high densities of *S. salpa* as a result of chemical defences against herbivory (Vergés et al. 2009).

Algae (particularly epiphytes) were also the dominant component consumed by the omnivorous *D. capensis* (over 55%V in all size classes). Although ephiphytic diatoms make up a large component of the gut contents of both species and are important as a food source for juvenile sparids (Sheppard et al. 2012), the $\delta^{13}C$ of epiphytes did not clearly overlap with the $\delta^{13}C$ values of either of the fishes. This likely indicates that other food resources, such as macroinvertebrates like polychaetes, with higher $\delta^{13}C$ values were preferentially digested and reflected in the juvenile sparid muscle tissue. It has been suggested that larger *D. capensis* and *S. salpa* on rocky reefs ingest macroalgae for their epiphytic diatoms, with green seaweed (*Ulva* spp.) passing through the gut undigested (Christensen 1978; Joubert and Hanekom 1980). In the western Mediterranean, young juvenile *S. salpa* graze on turf algae (primarily *Halopteris* spp.), sub-adults on erect algae (such as *Dicytyota* spp), while larger adults feed on seagrass (Havelange et al. 1997). Epiphytes have been found to mediate the selection of macrophytes by larger *S. salpa* in Mediterranean seagrass ecosystems, with *S. salpa* selecting and feeding on *Caulerpa prolifera* (green algae) as opposed to *Cymodacea nodosa* seagrass when epiphytes were removed from seagrass leaves (Buñuel et al. 2020). In contrast to seagrass, which is poorly digested (Havelange et al. 1997) fish are able to digest and assimilate algae (Raubenheimer et al. 2005).

The assimilation of *Laurencia* and coralline turf over other algae in both species may point to the high nutritional value and availability of carbohydrates from *Laurencia* and coralline turf. Herbivorous fish select algae based on available carbohydrate (Raubenheimer et al. 2005), the presence or absence of secondary metabolites and nutritional qualities, such as energy, micro-nutrients and protein content (Tolentino-Pablico et al. 2007). Both *Jania* and *Laurencia* are amongst the red algae selected and consumed by marine herbivorous fish globally (Tolentino-Pablico et al. 2007). As such, investigating the nutritional qualities of the macroalgae in the Algoa Bay nursery seascape would be an informative future research priority.

The omnivorous *D. capensis* dominate the fish assemblage on low profile reef and forage on prey resources at a

higher trophic level (higher $\delta^{15}N$) than *S. salpa* which are foraging on prey resources at a lower trophic level (feeding primarily on algae). Higher trophic level prey resources, such as polychaetes and then amphipods, typically fractionate to a higher $\delta^{15}N$ in the consumer organism (Bearhop et al. 2002; Kilham et al. 2009). This was confirmed by gut content analysis with the consumption of macroinvertebrates by *D. capensis* increasing from 19%V in the smallest 40–49 mm FL size class to 42%V in the next 50–59 mm FL size class.

Polychaetes, although not the most abundant macroinvertebrate recorded, were important in the diet of both *D. capensis* and *S. salpa*, with the greatest abundance and biomass of polychaetes associated with coralline turf. Polychaetes are able to swim but they spend most of their time in burrows (Thomsen and McGlathery 2005), with coralline turf providing close access to sediment and sedentary rock. Figueiredo et al. (2020) although overall finding a greater abundance and biomass of macroinvertebrates associated with canopy-forming *Sargassum* spp. and *Dichotomaria marginata* than algal turf, also found that soft-bodied invertebrates (polychaetes and flatworms) were more common within the turf habitat.

Canopy forming *P. corallorhiza* on high profile reef offers more refuge from predation (both in terms of cover and height) than low growing *Laurencia* and coralline turf algae, which together dominate low profile reef. Analysis of recent videos from shallow pebble reef dominated by coralline turf algae, adjacent to Flat Rocks, showed far fewer juvenile fish, with only a shoal of larger sub-adult/adult *S. salpa* seen feeding on the turf algae (Fig. S2). This suggests that although lower growing algae, such as coralline turf algae and *Laurencia*, may provide food for juvenile sparids, the structure provided by canopy-forming algae within a habitat mosaic is important for protection from predation and without structure for shelter juveniles may not select/use these habitats. We recently showed using artificial vegetation units, mimicking seagrass of different densities (but the same height), that juvenile *R. holubi* actively select dense seagrass over bare sediment and low cover seagrass (Welch et al. 2024). Similarly, Hinz et al. (2023) also using artificial vegetation units found that juvenile *Coris julis*, *Symphodus ocelatus* and *Diplodus vulgaris*, associated with more complex (height and fractal dimension) macrophyte configurations.

Interestingly, Hinz et al. (2023) mention that juvenile *D. vulgaris* are associated with heterogenous coastal habitats in general, which include rocks, seagrass and canopy-forming macroalgae, with solid structures, such as rocks also used as cover for these species. The endemic *D. capensis* is similarly associated with a range of heterogeneous coastal habitats in South Africa, including estuarine seagrass beds and rocky shores. Although it may be using canopy-forming *P. corallorhiza* for shelter, it may also be using the rocky outcrops in the high profile reef for shelter. Although we only recorded three piscivorous fish *Myliobatus aquila*, *Epinephelus marginatus* and *Uraspis secunda*, piscivorous birds can exert considerable predation pressure on sparids in shallow nursery areas, with piscivorous birds, for example, causing an 80% decrease in the population of juvenile *R. holubi* over a five-month period in a closed estuary (Blaber 1973). High cover of vegetated habitats have been shown to reduce the predation of fish by piscivorous birds (Tabor and Wurtsbaugh 1991).

Conclusion

Although much of the research on the nursery provision of macroalgae has focussed on the importance of canopy forming brown algae for both shelter and food, this study has shown that littoral rocky reef with a mosaic of both canopy-forming and low growing red algae provide high quality nursery habitat, in terms of both food and shelter, for juvenile sparids. This emphasizes the importance of macroalgal heterogeneity in nursery provision across a range of services including food resources and shelter.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-024-04506-2.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Aidan Jacobs, Nicola James, Mihle Gayiza, Gavin Rishworth, Lucienne Human and Paul-Pierre Steyn. The first draft of the manuscript was written by Nicola James and Aidan Jacobs with all authors providing edits.

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Data availability The datasets generated during and/or analysed during the current study are available on request.

Declarations

Ethical approval Research was carried out under the approval of the Nelson Mandela University animal ethics committee (Ethics number A20-SCI-ZOO-004) and according to the university's animal ethics guidelines.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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