Observations of the habitats and biodiversity of the submarine canyons at Sodwana Bay

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The discovery of coelacanths, *Latimeria chalumnae,* in Jesser Canyon off Sodwana Bay in northern KwaZulu-Natal in 2000 triggered renewed interest in the deep subtidal habitats associated with submarine canyons. Information stemming from three recreational Trimix diving expeditions in Wright and Jesser canyons between April 1998 and June 2001 revealed distinct and diverse invertebrate and fish communities in the canyons of the Greater St Lucia Wetland Park (GSLWP). In total, 69 invertebrate taxa were collected from Wright Canyon, including at least 15 new records for South Africa plus 11 potential new species and 16 range or depth extensions. Divers documented the first five coelacanth specimens and obtained information on fish distribution and abundance. Five different habitat types were recognized supporting distinct biological communities; the sandy plains outside of the canyons, scattered rock outcrops within the sandy plains, the canyon margin, canyon walls and caves and overhangs. The canyon margin is the richest habitat and supports dense communities of invertebrate suspension feeders, as well as a diverse and abundant fish fauna. Dominant canyon invertebrates included sponges, black corals, gorgonians, alcyonarian soft corals and stylasterine lace corals. These invertebrates support a diverse epifauna including basket- and brittlestars, winged oysters and other molluscs. The canyons within the GSLWP protect large populations of commercially important linefish species including the sparids, *Chrysoblephus puniceus, C. anglicus, Polysteganus praeorbitalis* and *P. caeruleopunctatus,* as well as several species of serranids and lutjanids. Additional biological sampling and standardized quantitative sampling within the canyons and deep reefs is required to develop a better understanding of their biological communities and the factors that shape them.

Introduction

Despite the worldwide distribution of hard-bottom communities in the deep subtidal, the deep reef environment is one of the least known marine habitats. Drowned reef communities, palaeoshorelines, submarine canyons, outer shelf and upper slope habitats and seamounts all constitute deep hard-bottom habitats. Scientific scuba diving is limited to depths less than 50 m and rocky areas beyond this depth are difficult to sample by dredge or trawl. Submersible-based research is conducted mostly beyond 150 m. This leads to a paucity of information on the habitats in the 50–150-m depth range, which are thought to host unique invertebrate communities and support commercially important fish species.[1–3] Recent exploration by Trimix diving in this depth range is uncovering many new species and expanding knowledge of reef ecology.[4] Trimix diving involves the use of oxygen-enriched air and helium to allow diving at extended depths.

In South Africa, there has been little research in the deeper subtidal habitats and our understanding of the non-fish fauna from this depth range has been described as poor.[5] Trawling and dredging have yielded some information about the fauna of soft bottom habitats, but the inaccessible rocky areas are poorly studied and information on community structure is particularly lacking. In 1991, the *Jago* submersible was used in an expedition to explore deep reefs in the Tsitsikamma National Park and near the site of the first coelacanth capture off the Chalumna River mouth on the South African south coast. However, no scientific publications emerged from this expedition and observations of fish and invertebrates were not documented.

Scuba surveys of invertebrate and ichthyofauna in the Greater St Lucia Wetland Park (GSLWP) in KwaZulu-Natal (KZN) have been confined to depths of less than 40 m.[6–8] The discovery of coelacanths, *Latimeria chalumnae,* in the canyons off Sodwana Bay[9] sparked an interest in the canyon environment of the GSLWP. Knowledge of these habitats is needed for management of marine resources and conservation planning. Deep rocky habitats support populations of commercially important reef fish species.[2,10] These fish are targeted by commercial and recreational fisheries outside of marine protected areas in KZN. In the last two decades, targeting of deep reef species have increased in KZN, reflecting that effort has shifted to deeper reefs.[10]

This study presents the first account of the physical and biological characteristics of two submarine canyons in the GSLWP, based on information collected by Trimix divers during two expeditions. The primary objective of the divers was to search for coelacanths, although divers were briefed on data collection and biodiversity sampling.

The Wright Canyon expedition was led by a trained biologist with supervision from marine scientists. The expeditions in Jesser Canyon had little scientific direction but accurate records; video footage and digital still images were made available to science. Interviews, records from logbooks, digital images and video and biological specimens were used to define habitat types, to examine invertebrate and fish diversity in the canyons and to explore patterns in biological community structure.

Study area

More than 20 submarine canyons have been mapped in the GSLWP on the northern coast of KwaZulu-Natal on the east coast of South Africa (Fig. 1).[11] This paper is based on information collected from expeditions in Jesser and Wright canyons situated approximately 4 km apart. The canyons break through the shelf at depths ranging between 90 and 110 m; their bottom (thalweg) has a depth of several hundred metres. Wright Canyon is a large feature and is classified as a mature canyon with a depth of more than 700 m, a maximum width of 2.2 km and steep gradients ranging from 24–60°.[11,12] It is located approximately 6 km north of Jesser Point at Sodwana Bay and breaches the continental shelf

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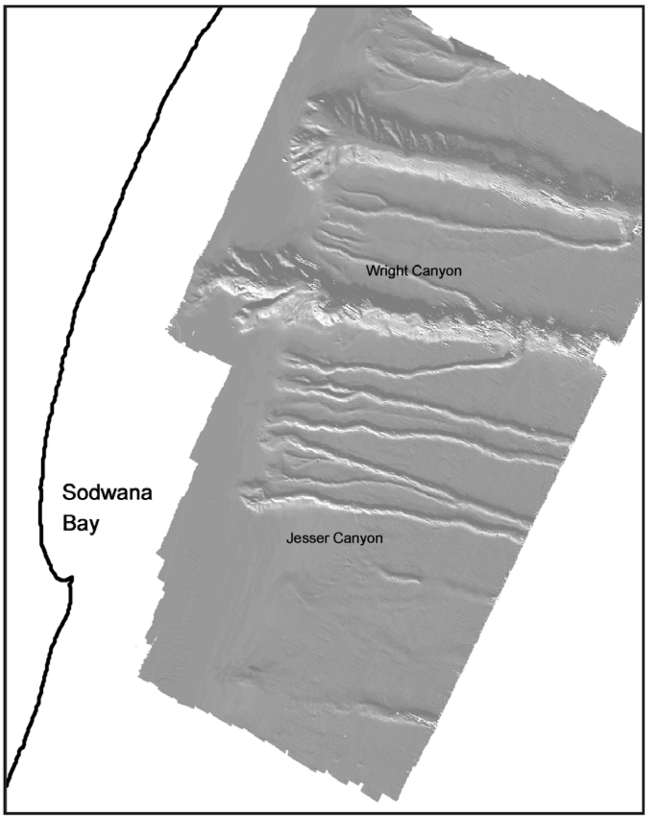

Fig. 1. Map showing the position of Jesser and Wright canyons off Sodwana Bay in the Greater St Lucia Wetland Park. The canyons are approximately 4 km apart.

approximately 2 km offshore. Jesser Canyon is classified as a youthful phase canyon that extends to depths of about 250 m.[11] In contrast to Wright Canyon, Jesser is a small lobate feature measuring less than 0.7 km across at the canyon head. Jesser and Wright represent two of the three canyons where coelacanths have been documented.[13]

Methods

The information presented here is based on data collated during a total of 19 exploratory Trimix dives between 1998 and 2001. Eight dives were undertaken in Wright Canyon at depths between 75 and 140 m in June 1998 (Table 1). Divers documented the topography of the sea floor, noted currents, and estimated percentage cover of living organisms. Surface and bottom temperatures were recorded from Mares M1 dive computers. Biological specimens were collected during eight dives and video footage from four dives was examined. A total of five dives was carried out in the southern lobe of Jesser Canyon in November 2000 and May 2001. As these dives focused mainly on the discovery of coelacanths, fewer details on the habitat were documented and no biological specimens were collected, but approximately 40 minutes of video footage were recorded.

Invertebrate samples

Invertebrate samples collected during the Wright Canyon expedition were identified using field guides and taxonomic papers.[7,15–25] Taxonomic experts were consulted when necessary. After identification, specimens were accessioned in the Iziko South African Museum in Cape Town or the Natal Museum in Pietermaritzburg, where they are housed within the marine invertebrate and mollusc collections, respectively.

Analysis of video footage

Four sequences of amateur video footage were available from Wright Canyon (Table 1, dives 2, 4, 5 and 6). Visibility was poor and only specimens that were lit with artificial light were identifiable. As each dive covered a separate habitat (four depths and different substrates), the dives cannot be considered as replicates and any analysis of general community structure for Wright Canyon (as was done for the Jesser Canyon margin) is inappropriate. A species list of fish and some estimate of their relative abundance was compiled.

Five video sequences from the coelacanth discovery in Jesser Canyon were examined to provide a general description of invertebrate and fish fauna. The five video transects were treated as replicate transects and macro-invertebrates and fish were counted for each dive to provide a preliminary assessment of relative abundance. Video sequences of benthic communities ranged from 8–14 minutes but only a standardized eight minutes, covering approximately 80 m, were analysed per dive. Each sequence was examined several times with only a single taxon counted each time. Changing camera focal lengths and the absence of any referenced size scale precluded the use of estimates of percentage cover or area.

PRIMER (Plymouth Routines in Multivariate Ecological Research, version 4.0, 1994) was used to explore patterns in the biological data from Jesser Canyon.[26] Data were root transformed to weight the contribution of less abundant species. Hierarchical clustering analysis using Bray-Curtis coefficients and multidimensional scaling (MDS) were used to examine similarity between transects. Characteristic species were identified using similarity percentage breakdown (SIMPER) analysis.[27]

Results

Current and sea temperature

Although strong surface currents were noted during the expeditions, divers never experienced any currents within

Table 1. Dive data for eight dives conducted in the vicinity of Wright Canyon and five dives conducted in Jesser Canyon in 2000/01.

Dive no.	Location*	Depth (m)	Date	Visibility (m)	Sea-surface temperature (and below thermocline) (°C)	Bottom time (min)	$n^{\dagger}$
1	27°29.361′S, 32°42.287′E	75	17 Jun. 98	40	23 (16)	10	34
2	27°29.361′S, 32°42.287′E	75	18 Jun. 98	40	23 (16)	10	0
3	27°29.361′S, 32°42.391′E	85	19 Jun. 98	5–10	24 (16)	10	3
4	27°28.700′S, 32°42.475′E	90	24 Jun. 98	20–40	24 (20)	15	15
5	27°29.568′S, 32°42.975′E	100	24 Jun. 98	20	23 (20)	10	3
6	27°29.568′S, 32°42.975′E	120	25 Jun. 98	30–40	22 (19)	8	15
7	27°29.361′S, 32°42.287′E	140	26 Jun. 98	20–40	22 (20)	8	21
8	27°29.223′S, 32°42.516′E	85–95	28 Jun. 98	10	22 (17)	10	21
9–13	Jesser Canyon	90–120	Nov. 00–May 01	20–40	(17–19)	10–14	0

*The site coordinates as determined by LCX-15mt Lowrance GPS.
†The total number of biological samples collected per dive.

either Jesser or Wright Canyon. Strong currents were confined to the top 30 m and no currents were noticed below 50 m. In Wright Canyon, sea-surface temperatures ranged between 22 and 24°C. Thermoclines were evident between 14 and 21 m during all dives, with bottom temperatures ranging between 16 and 20°C (Table 1). Surface temperatures were not documented in Jesser Canyon but, towards the bottom, temperatures declined to 17–19°C during all dives.

Topography

A general description of the topography of Wright Canyon was compiled from diver observations. Between 75 m and 90 m a gently sloping sandy area with scattered rocky outcrops was found. Features that were discovered included four large rocky domes (approximately 8 m tall and 15 m^2 in size) (Table 1, dive 1) and three rock outcrops about 10 m tall covering approximately 25 m^2 at 82 m. The rocky canyon margin was found at 90 m. From 95–140 m, divers reported that the canyon sloped steeply downwards with a gradient of 70–85° into a ravine with rocky and 'rubble' slopes and occasional patches of unconsolidated sediments. The rocky walls of the canyon slopes were highly eroded with high rugosity. Larger caves (approximately 1 m^2) and overhangs were reported during dive 8. Divers reported fine sediment covering the canyon walls. In Jesser Canyon, the sandy plains interface with the rocky canyon margin at approximately 95 m. The slope of the canyon walls was steep (30–50°) and heterogeneous with some areas with higher profile and rugosity and others covered with unconsolidated sediment. The divers documented two important features in the canyon walls at a depth of approximately 110 m. The first was a series of long narrow caves and overhangs, and the second was a shallow niche or U-shaped recess in the canyon wall. Coelacanths were sighted at both.

Invertebrate diversity

A total of 112 biological samples representing at least 69 taxa were collected from 70–140 m in Wright Canyon (Table 2). Of these, two were identified only to order level, eight to family level, 31 to genus level and 28 to species level. These specimens represent 47 families. Sponges were the group of invertebrates that featured most prominently in the invertebrate collection from Wright Canyon, with 27 specimens representing 21 taxa. Octocorals were the second most important phylum, with 10 taxa collected. Six of these were gorgonians and three were alcyonacian soft corals. Eight bryozoans representing six taxa were collected and several other epiphytic bryozoans were present on other specimens, particularly sponges. Five specimens representing four taxa of antipatharian black corals were collected. Several mobile invertebrates including molluscs, crustaceans and three echinoderms were sampled. Some specimens require further taxonomic work before it can be established whether their discovery represents new information. Seven of the specimens constitute extensions of the known depth range for particular species, nine represent range extensions and at least 15 constitute new records for South Africa. In addition, 11 samples appear to be new species. Many of the specimens requiring additional taxonomic work are also likely to constitute new records or new species.

Sponges

Prior to these collections, the number of documented sponges from deeper subtidal habitats (>50 m) off South Africa totalled approximately 40 species, most of which were recorded from trawls on the south and east coasts of South Africa during the early 1900s. Of the 20 species collected by the Trimix divers, six were previously reported from deep waters off the east coast (*Pachastrella monilifera, Hemistrella vasiformis, Hymeniacidon caliculatum, Topsentia pachastrelloides* and *Ircinia arenosa*), two from the west coast (*Poecillastra compressa, Clathria* (*Clathria*) *lissocladus*), and two from the south coast (*Pachastrella monilifera, Isodictya frondosa*). *Myxilla* (*Ectyomyxilla*) *kerguelensis* and *Hyppospongia nardorus* were recorded from depths of less than 50 m on the south and east coasts, respectively. The genus *Clathropella* is recorded for the first time in South Africa and the 10 other sponges appear to be new records or species for South Africa.

Hydrocorals

There is substantial taxonomic confusion in Milleporidae (fire coral) and Stylasteridae (lace coral) families and identification of the six hydrocoral taxa to species level is not feasible at present.[23] However, the three stylasterine lace corals represent new records as this family was not previously reported from South Africa.[5] Only two species of Milleporina corals are apparently known from South Africa[5] and the taxa collected in Wright Canyon appear to be distinct from these.

Octocorals

Ten taxa of octocorals were represented in the Wright Canyon collection. The gorgonian *Nicella dichotoma* represents a range extension and a new record for South Africa as this taxon was previously known only from Mauritius.[20] *Homophyton verrucosum* is a southern African endemic and is a common species in Maputaland in depths of up to 168 m,[7] whereas the grey gorgonian, *Rumphella* sp., was previously recorded at depths of less than 25 m.[7] A single *Junceella* sp. has been recorded from Sodwana Bay and the species collected in Wright Canyon is distinct from this, representing a new record and possibly a new species. The three alcyonacean soft corals all require further taxonomic work. *Chironephthea* is known from shallow water and the other specimens are not known. Several other unsampled soft corals were also evident in video footage. Only one seapen, *Pennatula murrayi*, was collected in Wright Canyon; this species has previously been collected in Maputaland.[7]

Antipatharian black corals and cerianthids

Until now, only three species of antipatharian black coral have been recorded in South Africa,[7] with three new taxa collected from Wright Canyon. In addition, other distinctive antipatharian species that are not represented in the marine invertebrate collection of the Iziko South African Museum were documented in canyon footage. The collection of a partial specimen of a tube anemone also represents a new record as cerianthids have not previously been recorded in South Africa.

Molluscs, crustaceans and echinoderms

The winged oyster, *Pteria loveni*, is a new record for South Africa and was collected at depths far greater than previously documented, 140 m instead of 30 m (R. Kilburn, Natal Museum, pers. comm.). The nudibranch *Chromodoris boucheti* found at 90 m was previously known only from depths of less than 35 m.[24] The only member of the nudibranch genus *Phyllidiella* sp. known from South Africa, *P. zeylanica*, is distinct from the specimen collected at 120 m at Wright Canyon and is known to occur to 25 m.[25] The unidentified *Stenopus* shrimp does not match the only species known from South Africa (*S. hispidus*) and should be sent for further taxonomic evaluation. The other crustaceans await further identification. The three echinoderm specimens

Table 2. List of invertebrate taxa collected in Wright and Jesser canyons.

Group	Family	Species	Wright Canyon depth (m)	Jesser Canyon depth (m)	Depth (#) or range (*) extension[†]	New record (+) or potential new species (++)[†]
Porifera	Pachastrellidae	*Poecillastra compressa*	90	100–110	*	
	Pachastrellidae	*Pachastrella monilifera*	75		*	
	Pachastrellidae	*Pachastrella* cf. *monilifera*	75			+
	Pachastrellidae	*Pachastrella* sp.	75–120			++
	Calthropellidae	*Clathropella* sp.	85			++
	Hemistrellidae	*Hemistrella vasiformis* var. *minor*	100–140			
	Hemistrellidae	*Hemistrella* sp.	75			++
	Halichondriidae	*Hymeniacidon caliculatum*	120			
	Halichondriidae	*Halichondria* sp.	100–140			++
	Halichondriidae	*Topsentia pachystrelloides*	90			
	Axinellidae	*Axinella* sp. 1	90			++
	Axinellidae	*Axinella* sp. 2	85			++
	Myxillidae	*Myxilla* (*Ectyomyxilla*) *kerguelensis*	90		#*	
	Isodictyidae	*Isodictya frondosa*	90		#	
	Microcioniidae	*Clathria* (*Thalysias*) *lissocladus*	90		#	
	Microcioniidae	*Clathria* (*Clathria*) sp. 1	75			++
	Microcioniidae	*Clathria* (*Clathria*) sp. 2	90			++
	Chaliniidae	*Haliclona* sp. 1	90			++
	Irciniidae	*Ircinia arenosa*	75	100–110		
	Spongiidae	*Hyppospongia nardorus*	75		#	
	Thorectidae	Unidentified sp. 1	75			++
Milleporidae	Milleporidae	Unidentified sp. 1	120			+
	Milleporidae	Unidentified sp. 2	75			+
	Milleporidae	Unidentified sp. 3	75			+
Stylasteridae	Stylasteridae	*Stylaster* sp. 1	140	100–110		+
	Stylasteridae	*Stylaster* sp. 2	90	100–110		+
	Stylasteridae	*Distichopora* sp.	90			+
Gorgoniacae	Ellisellidae	*Junceella* sp.	90	100–110		
	Ellisellidae	*Nicella dichotoma*	100–140	100–110		+
	Melithaeidae	*Leptogorgia* sp.	90	100–110		
	Anthothelidae	*Homophyton verrucosum*	75	100–110		
	Gorgoniidae	*Rumphella* sp.	75		#	
	Acanthogorgia	*Acanthogorgia* sp.	90	100–110		+
Alcyonacea	Nephtheidae	*Chironephthya* sp. 1	90		#*	
	Nephtheidae	*Siphonogorgia* sp. 1	75			+
	Nephtheidae	*Scleronephthya* sp. 1	75			+
Pennatulacea	Pennatulidae	*Pennatula murrayi*	75			
Hexacorallia	Dendrophyllidae	*Balanophyllia* sp.	75			
	Antipathidae	*Cirripathes spiralis*	90	100–110		+
	Antipathidae	*Cirripathes* sp.	90	100–110		
	Antipathidae	*Stichopathes* sp. 1	90	100–110		
	Antipathidae	*Antipathes* sp. 1	90	100–110		
	Cerianthidae	Cerianthus sp.	100			+
Mollusca	Limidae	*Lima nimbifer*	75			
	Pteriidae	*Pteria loveni*	140	100–110	#	+
	Mytilidae	*Septifer bilocularis*	75			
	Buccinidae	*Engina mactanensis*	75		*	
	Marginellidae	*Volvarina ingloria*	120		*	
	Trochidae	*Calliostoma layardi*	75			
	Nassariidae	*Nassarius* sp.	75			
	Coralliophilidae	*Coralliophila* cf. *squamosissima*	75			
	Phyllidiidae	*Phyllidiella* sp.	120		#	+
	Chromodoridae	*Chromodoris boucheti*	90		#	
Crustacea	Lysianassidae	*Trichozostoma remipes*	90			
	Diogenidae	*Dardanus* sp.	75			
	Galaththeidae	*Galathea* sp.	75			
	Hipiidae	Unidentified Brachyuran sp.	75			
	Dromiidae	Unidentified Dromid crab sp. 1	75			
	Portunidae	*Lissocarcinus orbicularis*	75			
	Stenopodidae	*Stenopus* sp.				++
Bryozoa		Unidentified ctenostome sp. 1	90			
		Unidentified ctenostome sp. 2	120			
	Phidoliporidae	Unidentified Phidoloporidae sp. 1	100–140			
	Phidoliporidae	Unidentified Phidoloporidae sp. 2	90			
	Tubiloporidae	*Idmidronea* sp.	100			
	Tubiloporidae	Cf. *Idmidronea* sp.	140			
Echinodermata	Asteroschematidae	*Asteroschema capensis*	140	100–110	*	
	Ophiotrichidae	*Ophiothrix proteus*	90	100–110		
	Gorgonocephalidae	*Astroba nuda*	70–120	100–110		

[†]# and * represent an extension of known range or depth, respectively. + and ++ indicate new South African records or potential new species, respectively.

Table 3. The ten most common macroinvertebrate taxa at depths of 100–110 m at Jesser Canyon margin as determined from SIMPER analysis of abundance data from five video transects. The ranking is determined by S_i, the average contribution of each species to the overall similarity of the area.

	Family	Species	Mean*	S_i/s.d.(S_i)[†]	ΣS_i%[‡]
1	Antipathidae	*Stichopathes* sp. 1	7.8	2.71	*29.4*
2	Antipathidae	*Stichopathes* sp. 2	1.8	1.09	*39.8*
3	Ellisellidae	*Nicella dichotoma*	5.6	0.62	*48.8*
4	Stylasteridae	*Stylaster* sp.1	1.2	1.14	*55.7*
5	Asteroschematidae	*Asteroschema capensis*	2.6	0.62	*61.6*
6	Phellodermidae	*Echinostylis* sp.	4.4	0.60	*66.7*
7	Ellisellidae	*Junceella* sp. 2	3.8	0.62	*71.6*
8	Diademnidae	*Diademnum* sp. 1	0.6	0.61	*75.4*
9	Phidoliporidae	Unidentified sp.	0.6	0.61	*79.0*
10	Stylasteridae	*Stylaster* sp. 2	0.6	0.61	*82.3*

*The mean indicates the average number of specimens for an 8-min transect covering approximately 80 m.
[†]S_i/s.d.(S_i) is the ratio of S_i and the standard deviation of S_i. This ratio reflects how consistently the species abundance varied over the area examined.
[‡]ΣS_i% is the cumulative percentage contribution of each species to the overall similarity, S.

are known from the area. The brittlestar *Asteroschema capensis* was previously recorded at depths of 110–132 m.[28] Video footage from both canyons showed that this brittlestar is commonly attached to the gorgonian *Nicella dichotoma. Ophiothrix proteus* is a well-known Indo-Pacific species occurring from the infralittoral to 112 m. Similarly, *Astroba nuda* has appeared in trawl samples in the Indo-Pacific.[28]

Video footage from Jesser Canyon also revealed dense and diverse invertebrate communities extending from the canyon margin to a depth of 110 m. Nine taxa in the Jesser Canyon footage were identified from specimens collected during the Wright Canyon expedition. A total of 34 macroinvertebrate taxa were recognized (Tables 2 and 3).

Fish diversity

A fish species list was compiled from video footage of both canyons (Table 4). A total of 18 species were documented in Jesser Canyon and 11 species in Wright. The poor quality of the Wright Canyon footage limited abundance estimates of each species to three broad categories: only one fish seen, between 3 and 20 individuals sighted, or more than 20 individuals observed. The five video transects for Jesser Canyon documented approximately 500 individual fishes representing at least 18 taxa (Table 4). These included large shoals of lutjanids and fusiliers (*Paracaesio* and *Caesio* spp.), small shoals of the one-stripe goldie, *Pseudanthias fasciatus,* as well as shoaling reef fish such as slinger, *Chrysoblephus puniceus.* Apart from slinger, other commercially important linefish species documented in the canyons were Englishman, *Chrysoblephus anglicus,* Scotsman, *Polysteganus praeorbitalis,* and blueskin, *P. caeruleopunctatus.* Divers also reported other species that did not feature on video footage. These included giant kingfish *Caraynx ignoblis,* cleaner wrasse *Labroides dimidiatus*, twotone wrasse *Thalassoma amblycephalum,* blood snapper *Lutjanus sanguineus,* and a tilefish *Hoplolatilus* sp., at 75–90 m adjacent to Wright Canyon. In addition, several unidentified fish appeared in footage or were reported by divers including two chaetodontids, a labrid, an unidentified anthiine fish and an apogonid.

The Trimix teams documented only one previously unrecorded taxon of fish in Jesser Canyon, the coelacanth *Latimeria chalumnae.* The Trimix divers documented five individual coelacanths in Jesser Canyon, each of which could be recognized by its unique spot pattern. These have been identified as individual numbers 1, 2, 3, 12 and 13 in the African Coelacanth Ecosystem Programme coelacanth catalogue.

Patterns in community structure

Five habitats were subjectively recognized in the deep subtidal environment of the GSLWP: (1) the sandy plains outside of the canyons, (2) scattered rock outcrops within the sandy plains, (3) the canyon margin, (4) canyon walls, and (5) caves and overhangs. These habitats have different abiotic features and host distinct biological assemblages. Deeper sections of the canyon including the thalweg were not examined, although these environments are also likely to constitute distinct habitats. Sufficient video footage for quantitative analysis was available only for the canyon margin.

Table 4. Checklist and relative abundance of fishes in Wright and Jesser canyons based on video footage taken in 1998 and 2000/01, respectively.

Family	Genus and species	Common name	Wright*		Jesser[†]		Known in Comoros?[‡]
			Abundance	Depth (m)	Mean	s.d.	
Monocentridae	*Monocentris japonicus*	Pineapplefish	–		0.4	0.5	yes
Holocentridae	*Myripristis chryseres*	Yellowfin soldierfish	2	85–110	0.8	1.3	yes
Scorpaenidae	*Scorpaena* sp.	Scorpion fish	–		0.2	0.4	yes
Serranidae	*Pseudanthias fasciatus*	One-stripe goldie	3	90–120	18.2	14.4	no
Serranidae	*Epinephelus marginatus*	Yellowbelly rockcod	1	75	0.6	0.5	no
Serranidae	*Epinephelus morrhua*	Contour rockcod	2	75–110	0.6	0.5	yes
Serranidae	*Epinephelus poecilinotus*	Dot dash rockcod	2	75–120	0.6	0.5	no
Serranidae	*Aulacocephalus temminckii*	Goldribbon soapfish	2	75–110	0.5	0.6	yes
Lutjanidae	*Paracaesio xanthura*	Yellowtail fusilier	–		55.25	72.3	no
Caesionidae	*Caesio* sp.	Unidentified fusilier	–		11.6	11.7	no
Sparidae	*Chrysoblephus puniceus*	Slinger	3	75–120	20.4	16.0	no
Sparidae	*Diplodus cervinus*	Zebra	2		0.6	0.5	no
Sparidae	*Polysteganus caeruleopunctatus*	Blueskin	2	75–120	0.75	0.5	no
Sparidae	*Polysteganus praeorbitalis*	Scotsman	2	75–120	0.5	1.0	no
Sparidae	*Chrysoblephus anglicus*	Englishman	–		0.25	0.5	no
Chaetodontidae	*Chaetodon marleyi*	Doublesash butterflyfish	1	95	–		no
Carangidae	*Seriola rivoliana*	Tropical yellowtail	–		0.5	1.0	no
Carangidae	*Caranx/Carangoides* sp.	Unidentified kingfish	–		0.8	1.8	no
Total					112.55		

*Because of poor video quality data for Wright Canyon, the relative abundance of fishes is expressed in one of three categories: 1, only one specimen seen; 2, >3 but <20 fish; 3, >20 fish observed.
[†]The abundance of fishes at Jesser Canyon is expressed as the mean and standard deviation (s.d.) for each species as determined from five video transects covering a distance of 50 m at depths of 105–110 m.

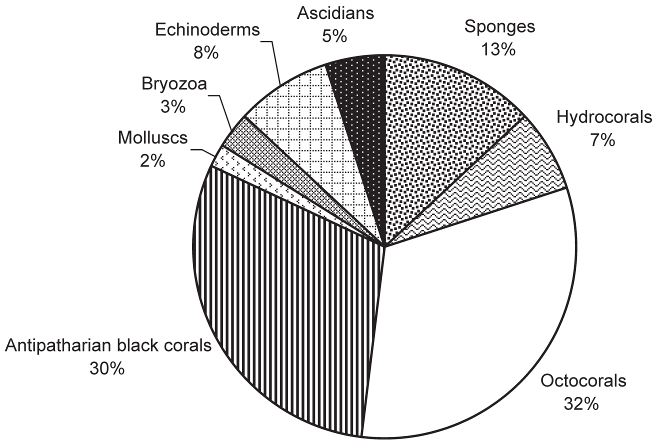

Fig. 2. The relative abundance of benthic invertebrates at Jesser Canyon margin as determined from counts of 34 taxa in five video sequences.

Sandy plains

The sandy plains were dominated by several taxa of seapens including *Pennatula murrayi, Virgularia* sp. and a *Cavernularia* sp. Other faunas reported from this habitat include large (*c.* 30 cm) unidentified crinoids and unidentified heart urchins. Divers reported bioperturbation within the patches of unconsolidated sediments with burrowing animals and mounds of shellgrit (400 mm tall) occupied by a tilefish, *Hoplolatilus* sp. (Table 1, dives 1–3). The only other fish identified in the sandy plains were blueskins, *Polysteganus caeruleopunctatus.*

Rocky outcrops

There was no footage of the rocky outcrops, but divers reported that these reefs host an invertebrate fauna different from that of the canyon margins. Large gorgonians were conspicuously absent and divers reported that sponges and bryozoans were the dominant invertebrates. Large sparids and serranids were observed in this habitat. The blood snapper, *Lutjanus sanguineus,* was observed only in this habitat.

Canyon margins

The canyon margins had the greatest density and diversity of both invertebrate and fish fauna. In Wright Canyon, the estimated cover of living organisms in the margin habitat was 80% (Table 1, dives 4, 5 and 6). The benthic community of the rocky margin of both Wright and Jesser canyons was dominated by filter feeders. In Jesser, octocorals and black corals were the dominant invertebrates (Fig. 2). Gorgonians, antipatharian black corals (*Stichopathes* and *Cirripathes* spp.), bryozoans and a diversity of sponges were documented in both canyons (Tables 2 and 3, Fig. 2). A conspicuous but less abundant asteroid that was seen along the canyon margins was the basket star *Astroba nuda.* Fish life was also most abundant at the canyon margin with reports and footage of shoaling fusiliers, lutjanids, carangids and sparids aggregating alongside the canyon edge. The large antipatharian black corals and gorgonians provide refuge for small fish, particularly *Pseudanthias fasciatus,* the dominant fish along the canyon walls. The degree of sedimentation also appeared to influence community structure with fewer species and individuals in sanded areas. The gorgonians, *Homophytum verrucosum* and *Rumphella* sp., and an unidentified reticulated bryozoan occupied heavily sanded areas.

The five video transects used for quantitative analysis were filmed at the Jesser Canyon margin. Exploratory analysis of the relative abundance of broad groups of invertebrates revealed extensive spatial variability within an area of less than 500 m^2. Hierachical cluster analysis revealed that the transects captured communities that showed similarities of 30–75% in terms of composition and abundance of taxa. SIMPER analysis revealed that the two most characteristic invertebrate taxa in this habitat were black corals of the genus *Stichopathes* (Table 3, as reflected by the ratio S_i/s.d.(S_i)). This was followed by the gorgonian *Nicella dichotoma* and two species of stylasterine lace corals. *N. dichotoma* is the second most common species in the margin but as its abundance is more variable it is less characteristic than *Stichopathes* sp.[2]

Caves and overhangs

Within the canyons, the cave and overhang habitat supported distinct biological assemblages. Lace corals (*Stylaster* spp. and *Distichopora* spp.) and delicate cyclostome bryozoa were found in the sediment-free inner areas of cave or overhang roofs. Different species of sponges and gorgonians including *Acabaria* and *Leptogorgia* spp. were documented in caves. The upper surface of overhangs and caves also supported distinct assemblages. These habitats had diverse and dense communities of sponges, octocorals (*Junceella* and *Ctenocella* spp.) and antipatharian sea whips (*Cirripathes* and *Stichopathes* spp.). Caves hosted different fish species including coelacanths, rockcods *Epinephelus* spp., yellowfin soldiers *Myripristis chryseres,* cardinals, *Apogon* spp., and pineapple fish, *Monocentris japonicus.*

Canyon walls

Both the observations of the Trimix divers and the video footage revealed a decline in the diversity and abundance or density of biota below 110 m. Estimates of living cover ranged from 15% to 50%. Below 120 m there was approximately 5% living cover on the rocky substrate and few fish were documented.

Discussion

The new information, records and species that emerged from this study were based on only 61 minutes of bottom time, indicating that the deeper subtidal habitats of the GSLWP represent a fertile area for new discoveries. The results were based solely on information collected by recreational Trimix divers, showing that this type of diving can be an effective means of sampling marine biodiversity at depths of 50–120 m. The results made it evident that the canyons of the GSLWP constitute distinct submarine habitats that support diverse invertebrate and fish communities different from those on inshore, coral-dominated reefs. A total of 69 invertebrate specimens were identified including several new records and potential new species. Fish species documented from video footage included the first five individuals of the African coelacanth as well as several commercially important line-fish species that are absent from inshore coral reefs. Five habitat types supporting distinct biological assemblages were subjectively recognized and patterns in community structure offer new insights into the ecology of the canyon environment.

Collection of invertebrates in the submarine canyons has increased our knowledge of benthic diversity in the deeper waters of South Africa. The biological specimens collected by the Trimix divers represent the first African invertebrates collected in this way from this depth range. In total, 15 new records and 11 likely new species emerged from this study. The known number of sponges below 50 m in South Africa was increased by 14 to a total of 54. The first South African representatives of stylasterine lace corals were collected[5] and new records of hydrocorals, octocorals and black corals were made. Invertebrate collections resulted in nine range extensions and seven depth extensions, reflecting that research in deeper waters has potential to expand our knowledge of the distribution and ecology of benthic subtidal species. In addition, several conspicuous but unidentified invertebrate species were evident in video footage.

The identification of material was difficult in terms of local availability of expertise, keys and literature. Sponges, molluscs and bryozoans were identified by local taxonomists and echinoderms were identified by experts from London. For 24 families, no assistance could be found in South Africa. This includes families belonging to groups such as soft corals and black corals, important taxa that constitute fish habitats in the canyon and other deep-water environments. This lack of taxonomic expertise in South Africa threatens our understanding of marine biodiversity.[5] This country clearly needs to cultivate expertise in invertebrate taxonomy and extend collecting efforts and systematic studies into deeper water. The echinoderm biodiversity in the deeper water is largely undocumented and warrants sampling. Further collecting effort and taxonomic work is also needed for black corals, octocorals and anemones.

The different sampling methods may explain some of the reported differences between canyons. For example, although sponges were the most-sampled phyla at Wright Canyon, they did not appear to be dominant in the deep reef community as captured by the video footage from Jesser (Fig. 2). Substrate sampling could reveal that sponges make up a larger proportion of reef cover in Jesser, because, on video, encrusting sponges are difficult to distinguish from rock. The fine sediment often covering reef areas may also conceal encrusting sponges. The abundance of different groups of samples in the collection may not reflect their relative abundance *in situ* as divers target larger, more charismatic specimens. Video footage provides more accurate information on community composition. However, without biological samples from the canyons, many of the taxa seen in video footage would have been impossible to identify. Future biological surveys should therefore include both specimen collection and standardized video transects or counts.

Sampling of the fish community within the canyons is likely to produce new records and uncover new species. Several fish that could not be identified were seen or captured on film. For example, the tilefish *Hoplolatilus* sp., noted in the sandy plains, cannot be identified without a specimen. There is only one species of *Hoplolatilus* recorded from South Africa and this is known only from postlarvae collected off the Cape Peninsula.[29] Deep-water collections from deep reefs (50–100 m) in Papua New Guinea, Samoa and Fiji made important contributions to fish inventories there and discovered several novel fish species.[4] In Palau, Trimix divers captured an average of seven new fish species per hour of bottom time.[4]

The deep subtidal habitats explored by Trimix divers host a fauna that is different from the inshore patch reefs of the GSLWP. These reefs support 43 genera of scleractinian corals and at least 11 genera of soft corals.[6] The dominant invertebrate fauna are zooxanthellate with scleractinian corals and octocorals of the genera *Lobophytum, Sarcophyton* and *Sinularia* constituting the most abundant taxa.[30] These zooxanthellate corals and octocorals are absent from the canyon habitats. The dominant invertebrates in the canyons are sponges, azooxanthellate octocorals and antipatharian black corals (Tables 2 and 3, Fig. 2). Differences in the invertebrate fauna from deep and shallow reefs have been observed elsewhere. Comparison between shallow (0–40 m) and deep (60–107 m) reefs in Jamaica revealed that the community composition differed markedly between these habitats.[1] For example, 60% of the sponge fauna there was restricted to deeper water.

Fish communities in the canyons were also distinct from those on inshore patch reefs. One of the most abundant fish was the one-stripe sea goldie, *Pseudanthias fasciatus,* which although widespread in the Indo-Pacific, was previously not known from the GSLWP. This species is seldom seen in South Africa and this has been attributed to its deep-water habitat.[25] Similarly, there are few South African records for the goldribbon soapfish, *Aulacocephalus temminckii.*[29] This species was not recorded from shallow reefs in the GSLWP,[8,18] although Trimix divers reported it from almost every dive in the present study. Other species that were found in the canyons but that are absent from inshore coral reefs[8] include commercially important sparids such as slinger *Chrysoblephus puniceus,* Englishman, *C. anglicus,* blueskin, *Polysteganus caeruleopunctatus,* and Scotsman, *P. praeorbitalis.* Depth-stratified linefishing has shown that these species are found on deeper reefs between 20 and 60 m.[2] The most common serranids in the canyons, *Epinephelus poecilinotus* and *E. morrhua,* have never been documented during dive surveys although *E. poecilinotus* is known from specimens caught by angling in deeper water in the GSLWP.[18] These results suggest that several fish species are restricted to reefs in deeper water.

Five habitat types each supporting distinct biological communities were subjectively recognized with the canyon margins hosting the most diverse and dense biological communities. The sandy plains outside of the canyons host different invertebrate fauna characteristic of unconsolidated habitats. In future these habitats need to be sampled by dredge or box cores to facilitate the proper identification of biota. Sampling areas different distances away from the canyons may elucidate whether the canyons and the plains are linked and whether plains adjacent to the canyons host different communities from those in more uniform areas away from canyons. Divers reported that some taxa (such as gorgonians) were absent from deep reefs and rocky outcrops and other taxa confined to this habitat (e.g. *Lutanus sanguineus*). However, this habitat is poorly sampled and no images were available to investigate adequately the hard-bottom habitats in the 30–80-m range. Quantitative data are needed for deep reefs and outcrops to assess how distinct these habitats are from both the canyon margins and inshore reefs. Some species were confined to caves within canyons, although until caves within the deep reef systems are investigated we cannot determine whether these habitats are distinct within and outside of the canyon environment. Further work is needed at habitats from similar depth ranges elsewhere on the continental shelf of the east coast before meaningful comparisons of the invertebrate fauna can be made.

Analysis of invertebrate community structure in the Jesser Canyon margin showed extensive spatial variability within this habitat. This patchy distribution of organisms suggests that they may compete intensively for rocky substrate. The abundance of sponges, octocorals and black corals could be linked to reduced competition from photosynthetic species. Gorgonians are considered to occupy areas of reef where there is less competition from scleractinian corals and zooxanthellate octocorals.[7]

An increased food supply may also account for the abundance of suspension feeders at the canyon margin. Divers reported that large gorgonians and other suspension feeders were generally more abundant there than at the scattered reef outcrops outside of the canyons. This pattern may be related to the geology, oceanography and productivity of the shelf environment and may be important in understanding the energy flow in the submarine habitats of the GSLWP. The canyons may induce topographic upwelling that could drive primary production in this habitat. Patterns in fish abundance also support this idea. The most abundant fish along the canyon margins were planktivorous: fusiliers, lutjanids and the small serranid *Pseudanthias fasciatus.* In the Caribbean, fish communities from reefs at depths of 80–150 m are also dominated by small serranids and other planktivores that then support large predatory fish including serranids.[3,31] The planktivorous species of the canyon margins in the GSLWP may constitute important prey items for serranids and other large piscivores including coelacanths.[3,32]

There is some similarity in the deep subtidal fish community in the coelacanth habitat on the slopes of Grande Comore and in the canyons of Sodwana Bay. The fish families most frequently observed by the *Jago* in the 80–200 m zone of the coelacanth habitat of Grande Comore were also documented by Trimix divers in the Sodwana coelacanth habitat.[33,34] Additional fish families that were captured included several sparid species and representatives of the Carangidae, Chaetodontidae and Caesionidae. The preliminary indications of relative fish abundance in Jesser Canyon cannot be relied upon as accurate fish density data as this information was drawn from recreational diver footage and not standardized, replicated transects designed to assess fish density. Despite the preliminary nature of the abundance data, the large numbers of commercially important sparids in the canyons is noteworthy. It indicates that the canyon margin habitats in the GSLWP may play an important role in sustaining populations of these species. These results also suggest that the known coelacanth habitat in South Africa supports a greater density of fish than their habitat in the Comoros.[33,35] In the Comoros, coelacanths are reported to inhabitat a deeper depth range than in the GSLWP and with a low potential prey density. However, potential prey density was shown to increase with depth,[33,34] with a maximum density of 8.2 fishes or 7.2 potential prey per 100-m transect found in the 320–360 m zone. The Comoran surveys included almost 10 km and were conducted at night and are therefore not strictly comparable to those taken from the Sodwana video footage. Comparative quantitative benthic surveys and fish counts in South Africa, the Comoros and at other known coelacanth capture sites along the East African mainland and Madagascar would give new insight into the biological habitat of *Latimeria chalumnae.* This is particularly relevant as the distribution of prey species has been cited as a factor limiting the distribution and abundance of the coelacanth.[14,33,34]

Most of the information that emerged from this study was based on video footage and collections concentrated in two habitats, the canyon margin and caves and overhangs. Further biological sampling coupled with standardized quantitative surveys of different habitat types would allow proper comparison of their respective communities. Comparison of the invertebrate and fish fauna of the deep reefs outside of the canyons, the shelf edge and the canyon margin would be particularly interesting and could offer new insight into the underlying determinants of community structure in these deep subtidal habitats. To assess whether the canyons enhance productivity, shelf break biota should be compared between and within canyons. Future surveys should also include deep reefs, shelf edge and canyons outside of the GSLWP. Such comparisons are necessary to assess human impacts in unprotected areas. Furthermore, comparisons within versus outside of the GSLWP are required to determine the role of the park in maintaining deep-water biodiversity and sustaining populations of commercially important linefish species.

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