The South African coelacanths — an account of what is known after three submersible expeditions

Karen Hissmann[a,b*], Hans Fricke[b], Jürgen Schauer[a,b], Anthony J. Ribbink[c], Mike Roberts[d], Kerry Sink[c] and Phillip Heemstra[c]

Using the manned submersible *Jago*, the habits, distribution and number of coelacanths within all main submarine canyons of the Greater St Lucia Wetland Park were studied during 47 survey dives, with a total bottom time of 166 hours at depths ranging from 46 to 359 m, between 2002 and 2004. Twenty-four individuals were positively identified from three of the canyons, primarily from inside caves at or close to the canyon edges at depths of 96–133 m with water temperatures between 16 and 22.5°C. The population size of coelacanths within the canyons is assumed to be relatively small; coelacanths are resident but not widespread nor abundant within the park.

Introduction

For more than 40 years, it was assumed that the Comoros Archipelago, located in the Western Indian Ocean between Mozambique and Madagascar, was the only natural home of the living coelacanth. Specimens that were caught off East London,[1] Mozambique[2] and Madagascar[3] were assumed to be strays swept away from the Comoros by the powerful currents along the coast of eastern Africa.[4] Between 1995 and 2001, four coelacanths were caught off the southwest coast of Madagascar (R. Plante and B. de Gaulejac, pers. comm.), and additional specimens were recently caught in bottom trawl and deep-water shark nets off Kenya[5] and Tanzania.[6] With each occasional catch it became doubtful that these fish were all recent strays from the Comoros. In November 2000, the discovery of a group of coelacanths by scuba divers in submarine canyons off South Africa[7] demonstrated that Western Indian Ocean coelacanths are not restricted to the Comoro Islands.

South African coelacanths are found in an area that is located within the sphere of influence of the Agulhas Current, one of the strongest ocean currents in the world.[8] The physical environment therefore initially seemed to be different from the conditions found for the Comoran coelacanth habitat. The divers sighted the fish at the edge of Jesser Canyon at 100 m, almost 100 m shallower than the depth at which coelacanths live at the Comoros.[7] Finding coelacanths at different locations provides opportunities for comparative studies on the ecological requirements of the fish, lifestyle and activity patterns at different habitats, and on genetic similarities and differences between and within populations.

Most information on the life history and ecology of the living coelacanths known to date has been derived from *in situ* observations at Grand Comoro,[9–13] the largest island of the volcanic archipelago. The results of these studies were used to design coelacanth surveys in Indonesia[14] and South Africa as part of the African Coelacanth Ecosystem Programme.

The primary objective of surveys in South African waters was to assess the distribution and number of the coelacanths in the canyons of the Greater St Lucia Wetland Park (GSLWP) World Heritage Site. This census should assist the authorities in compiling a management plan for the conservation of a fish that is, on the one hand, accessible for specially trained sport divers and, on the other, ranked as rare and endangered[15] and therefore requiring protection. Determination of whether the group of coelacanths observed by the divers is resident in the Sodwana canyons and whether they constitute a viable population was a further important investigation. Acoustic telemetry of a single tagged fish gave insights into activity and movement patterns. Scale samples taken off coelacanths *in situ* by the submersible provided small amounts of tissue for genetic analyses. We summarize present understanding of the ecology and behaviour of the Sodwana coelacanths compared with findings from other locations.

Methods

Diving facilities

Coelacanths of the Comoros and South Africa usually live at depths of and below 100 m. The study of coelacanths thus requires sophisticated technology like manned submersibles, remotely operated vehicles (ROVs) or specially trained deep-water divers with mixed gas or re-breather equipment. The German research submersible *Jago*, which has an operating depth of 400 m, was used in extensive surveys off Sodwana (Fig. 1). The high manoeuvrability of the craft and an extensive bottom time, both essential for searching large areas and to inspect narrow niches, caves and overhangs, make *Jago* an ideal tool for coelacanth surveys. The submersible was operated from the FRS *Algoa*, which was modified for this purpose by the South African Department of Environmental Affairs and Tourism.

Study site

The marine protected area of the GSLWP contains 12 large and numerous small submarine canyons that run perpendicular to the shore along a stretch of coastline approximately 78 km in length. The canyons were identified and mapped by means of a multibeam bathymetric survey in 2002.[16] Canyon heads breach the continental shelf at distances of 2–4 km from shore at depths of 90–120 m. For more details on the geomorphology of the canyons, see Ramsay and Miller in this issue.[16] Table 1 lists the 13 canyons explored.

Coelacanth census and behavioural observations

From observations at the Comoros it is known that coelacanths spend the day in caves,[11] where they are usually exposed to water temperatures of about 20°C or less. The search for coelacanths off South Africa therefore focused within the same temperature range on those areas likely to have caves or other shelters. Caves and overhangs were located by cruising along a set depth

[a]Leibniz Institute for Marine Sciences, 14148 Kiel, Germany.
[b]Max-Planck-Institut für Verhaltensphysiologie, 82319 Seewiesen, Germany.
[c]South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6140, South Africa.
[d]Marine and Coastal Management, Ocean Environment Section, Private Bag X2, Rogge Bay 8012, South Africa.
*Author for correspondence. E-mail: khissmann@ifm-geomar.de

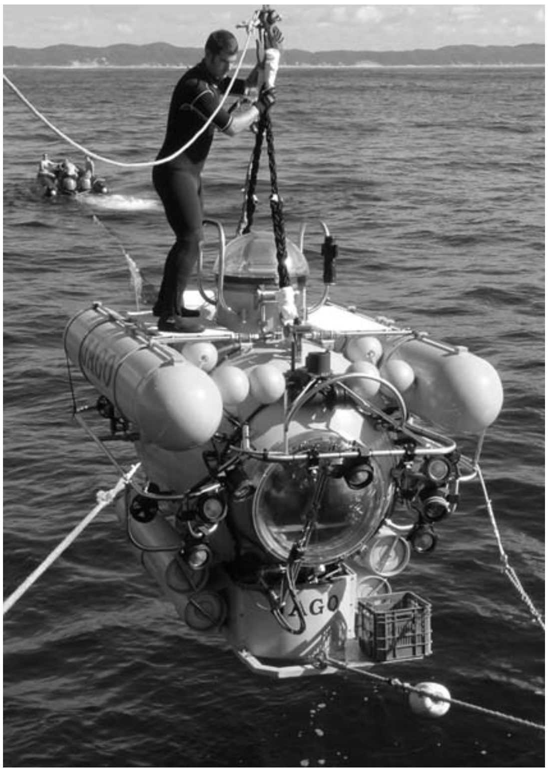

Fig. 1. Research submersible *Jago* being launched off Sodwana Bay from the FRS *Algoa.* (Photograph: James Stapley.)

contour mainly without artificial light to increase the range of vision in twilight.

All encounters with coelacanths were documented on video for later individual identification. From studies at the Comoros it is known that coelacanths show fidelity to various caves, which they visit regularly over several years.[12] Resighting known individuals allows investigations of home range, movement, space utilization, intra-species interaction, group composition and life patterns.[11,12]

In order to follow the coelacanths' nocturnal movements, the German team developed a minimally intrusive method to tag fish *in situ* from the submersible.[17] A depth-encoding ultrasonic transmitter is applied by dart to the fish by a pneumatic gun attached to the submersible's manipulator arm. The tag falls off after few weeks. The acoustic signals emitted by the tag are detected at the surface by a directional hydrophone connected to a depth-decoding ultrasonic receiver. Horizontal movements of the tagged fish are plotted by GPS at maximum signal strength. Off Sodwana, tracking was conducted from an inflatable boat and from the FRS *Algoa.* Most tracking took place at night when coelacanths are known to be more active,[18] with a few fixes taken on fish position during the day when possible.

Collection of environmental data

Data on the physical environment of coelacanths were collected during each dive by a temperature sensor attached to the submersible's keel and by a CTD (conductivity, temperature, depth) device at *Jago*'s stern. The CTD continuously recorded depth, temperature, salinity, oxygen and conductivity at intervals of 20 s. Visual observations of particulate floating matter, flexible soft corals, and other sessile animals revealed preliminary information on currents within the coelacanth habitat. No quantitative measurements of currents inside the canyons were available.

Visual and video observations were used for a preliminary assessment of fish density and species identification within the coelacanth habitat. A detailed account of the fish community supported by the canyon habitats off Sodwana is presented in this issue.[19,20] Fish counts were also conducted to estimate the abundance of potential prey fish (coelacanths are piscivorous) during the 2004 cruise, but results are not yet available. The extensive surveys for coelacanths provided valuable data on the biodiversity of the megabenthos and fishes within the coelacanth habitat and also geomorphological information. Two preliminary reports on the coelacanth habitat and the canyon morphology were compiled by the first author after the 2002 and 2003 cruises (unpublished reports, listed after references).

Scale sampling

Tissue samples were required for study of population genetics, genome and stable isotope analysis. Coelacanths possess large scales that overlap. The pigmented epithelium that covers the exposed part of the scale is a sufficient source for nuclear-DNA analysis. The *Jago* team developed a non-injurious method to collect scales from coelacanths in their natural environment. It includes a 60-cm-long cylindrical steel barrel mounted on the submersible's manipulator arm, a 70-mm-long cylindrical PVC dart that carries three short barbed tips at one end, and a 60-cm-long nylon string that connects the projectile with the air gun. The projectile is shot at the tail or flank of the fish from a distance of about 20 cm from the end of the barrel. The barbs penetrate only the thick scales. A short pull on the nylon line is sufficient to dislodge the scales from the fish. Because the scales overlap, up to three scales can be collected with a single shot. It is not possible to recover the scales and reload the air gun at depth, hence only one fish can be sampled during a dive. As soon as the submersible surfaced, the scales were taken to the ship and immediately processed for genetics (liquid nitrogen), genome

Table 1. Coelacanth survey dives within the canyons of the St Lucia Marine Protected Area in 2002, 2003 and 2004. Canyons are listed from north to south.

Canyon	Total no. of dives	Year	Bottom time (h)	Min.–max. depth (m)	Comments
Island Rock	1	’03	4.9	61–144	Some caves
South Island Rock	2	’02, ’04	6	81–198	Some caves
Mabibi	1	’02	3.6	110–135	Some caves
South Mabibi	2	’04	6	76–139	Very few caves
White Sands	2	’02, ’04	6.6	91–152	Very few caves
Wright	14	’02, ’03	35.9	46–345	Coelacanths
Unnamed	2	’02, ’04	8.9	95–193	Not suitable
Jesser	15	’02, ’03, ’04	54.3	70–255	Coelacanths
Diepgat	2	’02, ’04	12.6	50–359	Very few caves
Leadsman North	1	’04	5.4	94–184	Few caves
Leadsman South	1	’03	5.2	91–170	Some caves
Leven	2	’04	10.8	71–125	Some caves
Chaka	2	’04	6.3	70–124	Coelacanths
	47		166.4	46–359	3 canyons with coelacanths

studies (development of on-board cell lines) or stable isotopes (frozen). Re-sightings of coelacanths from which scales were removed during the present and previous expeditions allowed assessment of long-term effects of scale sampling. Similarly, studies in the Comoros have shown that dislodged scales re-grow with no ill-effect on coelacanths.[17]

Results

Habitat

Submersible surveys in the canyons of the GSLWP took place in 2002 (31 March–19 April), 2003 (19 April–3 May) and 2004 (21 April–6 May). In total, 47 survey dives with 166 hours of bottom time at water depths between 46 and 359 m were accomplished (Table 1). All dives were conducted in the vicinity of and inside the canyon heads during the day, where the probability of finding coelacanths in caves was greatest.

Structures suitable as shelters for coelacanths and water temperatures of 16–20°C were found mainly between 90 and 130 m, which were at and just below the canyon edges; most time was therefore spent searching within this depth range. Three dives to explore the canyon margins down to the canyon floor were made to maximum depths of 260 m in Jesser, 350 m in Wright and 359 m in Diepgat canyons.

Dives per canyon and year are listed in Table 1. All of the 12 main canyons were surveyed at least once, as well as three of the five unnamed smaller canyons between Jesser and Wright. Medium-sized canyons like South Island Rock, Mabibi, South Mabibi, Jesser and Chaka were explored almost completely within the priority depth range. The branched heads of Wright, White Sands, Diepgat, Leadsman North and South, and Leven are too large to be explored completely in the time available. Accordingly, surveys focused on priority areas that were selected according to their structural complexity on the bathymetric charts. In total, about 40 km of canyon slope was explored.

The canyon edges are usually distinct drop-offs situated between 90 and 135 m; approached from shore, the canyon edges are obvious from the increase in rocky structures and fish abundance. Almost all canyons except the unnamed ones between Jesser and Wright possess at least some caves that could accommodate coelacanths. Some of these caves were situated just below the canyon edge at about 100 m depth, others were found along the canyon walls down to 160 m.

The caves are of varying sizes and shapes (Fig. 2). Some large caves penetrate 6 m or more into the slope and are several metres wide and high, others are lower and less spacious. The cave entrance is usually as wide as the main compartment. Some caves have smaller chambers in their ceiling or walls. The cave roof and walls consist of karstic carbonate rock that is characterized by a rugged surface with sharp ledges and grooves. The cave floor is rocky or sandy, and sometimes covered with soft silt.

Coelacanth encounters

Coelacanths were successfully re-sighted in Jesser Canyon on the first dive in 2002, the canyon where they had been discovered by divers in 2000. The fish were also found in three of the 12 canyons explored (25%): Jesser, Wright and Chaka (Table 2). Jesser and Wright are situated about 4 km apart in the centre of the mapped area, just off Sodwana Bay. The unnamed small canyons between Jesser and Wright lack distinct canyon heads and caves and are considered unsuitable coelacanth habitat. The head of Jesser Canyon, one of the smaller to medium-sized canyons, is 400 m wide. Wright Canyon, in contrast, is one of the largest canyons off Sodwana, with a head that has several

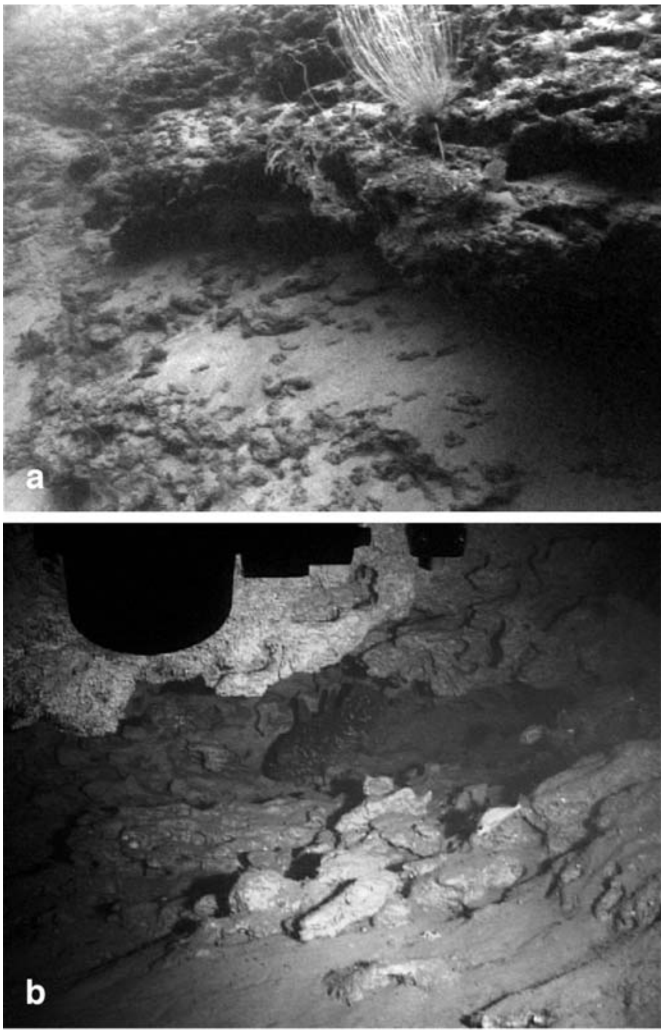

Fig. 2. Submarine cave at the edge of Jesser Canyon: (**a**) external view and (**b**) view inside with single coelacanth hovering at the back. Note karstic surface of rocks.

distinctive branches and a width of about 1700 m. Chaka, the southernmost canyon identified within the boundaries of the park, has a head width of about 700 m and is similar to Jesser in its structural complexity. These two canyons are about 48 km apart, with four large canyons (Diepgat, Leadsman North and South, and Leven) and a large area not known to possess canyons in between.

With one exception, all coelacanths were located in or near caves, overhangs or boulders. Occupied caves were located at depths between 96 and 133 m. One individual crossed *Jago*'s path, swimming downslope close to the bottom at 10:00, which was the only occasion when a coelacanth was found on open terrain during daytime. Another animal was encountered between large boulders at 144 m, the deepest record for a coelacanth off Sodwana.

In Jesser Canyon, coelacanths were found at three different caves located at the northern (cave 1, 103 m), western (cave 3, 125 m) and southern slope (cave 2, 113 m), and in an area with large boulders in the centre of the southern part (144 m).

In Wright Canyon, coelacanths occurred in seven well-separated caves along the canyon flanks: one cave at the northern slope (cave 1, 103 m), four within the western canyon arm (cave 4, 96 m; cave 5, 106 m; cave 6, 130 m; cave 7, 116 m), and two caves in the southern arm (cave 2, 133 m; cave 3, 107 m).

In Chaka Canyon, coelacanths occupied three different locations, all of them at the southern slope (cave 1, 103 m; cave 2,

Table 2. Details of coelacanth encounters within submarine canyons of the St Lucia Marine Protected Area during *Jago* dives in 2002, 2003 and 2004. The three individuals that have been seen exclusively by the divers are not listed.

Date	Location	Depth (m)	Temp. (°C)	No. of animals	Individual
31-03-02	Jesser, cave 1	103	19	1	1
03-04-02	Jesser, cave 2	111–113	18–19	7	1, 2, 3, 4*, 5, 6, 7
04-04-02	Jesser, cave 2	111–113	16.5	1	4*
13-04-02	Wright, cave 1	103	18.5	1	8*
14-04-02	Jesser, no cave	120	18	1	9
14-04-02	Jesser, cave 2	111–113	18.5	1	10
17-04-02	Wright, cave 2	125–133	16–19	2	1*, 11
19-04-02	Jesser, cave 1	103	18–19	1	4
19-04-03	Jesser, cave 2	111–113	–	4	1, 2, 3, 4
20-04-03	Jesser, boulders	144	17	1	1
20-04-03	Jesser, cave 2	111–113	19	2	4, 7
21-04-03	Jesser, cave 2	111–113	18	1	4
22-04-03	Jesser, cave 2	111–113	18	2	4, 14
23-04-03	Wright, cave 2	125–133	16	2	14*, 15**
23-04-03	Jesser, cave 2	111–113	17	2	2, 4
25-04-03	Wright, cave 2	125–133	17	1	16*
26-04-03	Wright, cave 3	107–112	17	1	15
26-04-03	Jesser, cave 2	111–113	18	4	4, 7, 14, 17
27-04-03	Jesser, cave 2	111–113	16	4	4, 7, 14, 17
29-04-03	Wright, cave 4	96	17	1	15
30-04-03	Wright, cave 5	106	16	1	18*
02-05-03	Wright, cave 6	130	16	1	15
24-04-04	Chaka, cave 1	103	17	1	20
24-04-04	Chaka, cave 2	114	18	1	21
27-04-04	Jesser, cave 3	125	22.5	5	1, 2, 3, 7, 22
06-05-04	Chaka, cave 3	118	19.5	3	20, 23, 24
16 different locations		96–144	16–22.5	52 encounters	21 individuals

*Scale sampled, ** tagged with ultrasonic transmitter.

114; and cave 3 below boulders at 118 m).

In all three canyons, as well as in some of the other canyons like Island Rock, South Island Rock, Mabibi, Leadsman South and Leven, numerous caves that appeared suitable for coelacanths were inspected but were not inhabited by the fish. Some of the medium-sized and larger canyons like South Mabibi, White Sands, Leadsman North and the large Diepgat Canyon have almost no shelter sites within the surveyed depth range and are considered less suitable coelacanth habitat.

Some of the caves occupied by coelacanths were inspected several times during each cruise. Cave 2 in Jesser, where the first coelacanths were documented by divers in 2000 and 2001, was checked four times in 2002 and was found to be empty once. In 2003, this cave was inspected seven times and was always occupied. In 2004, it was inspected twice and found to be empty both times. Another cave on the northern flank of Jesser at 103 m (cave 1), which was occupied twice in 2002, was empty on four inspections in 2003 and empty on one inspection in 2004. A cave in the southern arm of Wright Canyon, known as a coelacanth cave from 2002, was examined seven times in 2003 and occupied only twice (occupation rate of 29%). Jesser cave 3, inspected four times in 2003 and twice in 2004 was occupied only during the last visit in 2004. This shows that certain caves, like cave 2 in Jesser, are regularly occupied, whereas other, apparently equally suitable caves are less frequently inhabited.

The relatively low number of coelacanth sightings in 2004 compared to 2002 and 2003 (Table 2) is ascribed to the fact that most dives were performed in canyons other than Jesser and Wright; Wright was excluded as it was declared a coelacanth sanctuary.

Coelacanth identification

Individual coelacanths, including some fish seen only by divers, were catalogued based on their characteristic pattern of white spots (Fig. 3). To date, 24 individuals have been recognized

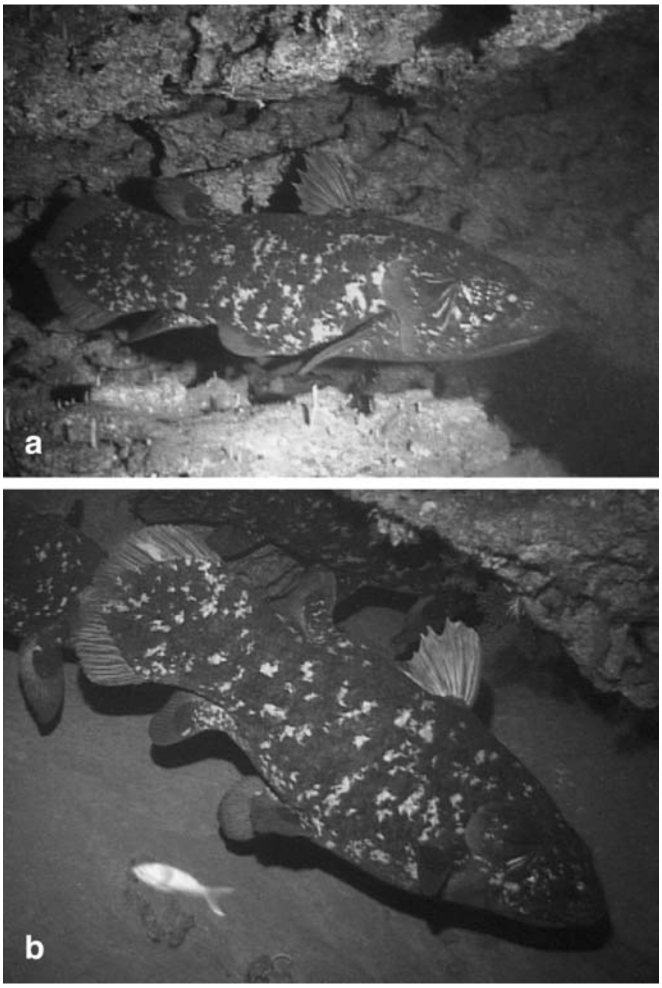

Fig. 3. Coelacanths off Sodwana Bay, (**a**) 'Jessy', or individual 1, seen regularly in Jesser Canyon since 2000; (**b**) the large individual 6, very likely a pregnant female.

Table 3. List of coelacanths identified and re-sighted between 2000 and 2004 within the submarine canyons off Sodwana Bay, South Africa.

Individual	Location	No. of sightings	2000*	2001*	2002	2003	2004
1	Jesser, Wright	8	x	x	x	x	x
2	Jesser	5	x	–	x	x	x
3	Jesser	4	–	x	x	x	x
4	Jesser	10	–	–	x	x	–
5	Jesser	1	–	–	x	–	–
6	Jesser	1	–	–	x	–	–
7	Jesser	5	–	–	x	x	x
8	Jesser	1	–	–	x	–	–
9	Jesser	1	–	–	x	–	–
10	Jesser	1	–	–	x	–	–
11	Wright	1	–	–	x	–	–
12*	Jesser	1	–	x	–	–	–
13*	Jesser	1	x	–	–	–	–
14	Jesser, Wright	4	–	–	–	x	–
15	Wright	4	–	–	–	x	–
16	Wright	1	–	–	–	x	–
17	Jesser	2	–	–	–	x	–
18	Wright	1	–	–	–	x	–
19*	Deep reef	1	–	–	–	–	x
20	Chaka	2	–	–	–	–	x
21	Chaka	1	–	–	–	–	x
22	Jesser	1	–	–	–	–	x
23	Chaka	1	–	–	–	–	x
24	Chaka	1	–	–	–	–	x
		59	3	3 (1)†	11 (8)	10 (5)	10 (6)

*Three individuals (*) were exclusively seen by the divers.
†Total number of new sightings each year given in brackets.

off KwaZulu-Natal (Table 3)[†]. Three of the five fish that were documented by the discovery divers in November 2000 and May 2001 were re-sighted in Jesser Canyon on every cruise. All re-sightings from previous years in 2003 took place in the most frequently occupied cave in Jesser, cave 2. In 2004, four of the new fish were documented in Chaka Canyon, which had not been explored before; the other animal was a new sighting from Jesser.

In total, nine of the 24 coelacanths identified to date off Sodwana were seen more than once (38%). The re-sightings over several years show that the Sodwana coelacanths are site-attached and resident within the canyon habitat, some of them for at least four years.

Body size, sex, and notable features

All coelacanths encountered in the GSLWP were adults with estimated total lengths ranging between 120 and 180 cm; consequently, none of these fish can be considered juvenile. Some of the individuals were large and appeared to be females, of which at least two might have been gravid as indicated by their enlarged bellies (Fig. 3b). Anatomical studies reveal that female coelacanths are generally larger than males.[21] Both large and medium-sized individuals were found together, suggesting that aggregations consist of both males and females.

All individuals appeared healthy with no sign of injuries or disease. One specimen (individual 8) had a slight deformity on all four of the paired fins. The amount of skin between two fin rays was enlarged, perhaps because of missing rays.

Another specimen (individual 18) had a small deformity at the upper lobe of the main caudal fin. The most anterior fin rays were either enlarged or completely missing, and this part of the fin flapped to the side and could not be kept erect. Two specimens had a relatively short supplementary caudal fin that did not protrude beyond the posterior edge of the main caudal fin.

The colouration of the Sodwana coelacanths does not differ from the Comoran coelacanths. In the Comoros, the white blotches on the blue-grey skin closely matches the white oystershell and sponge pattern scattered on the black basaltic cave walls. In South Africa, the limestone cave walls have a mottled pale appearance and the coelacanths' white blotch pattern does not provide the same degree of camouflage as in the Comoros, although it does disrupt the body profile to some extent.

Behaviour

Coelacanths were encountered as single individuals (15 occasions, 58%) or in aggregations (11 occasions, 42%). The largest number of coelacanths found together in 2002 was seven animals, in 2003 four and in 2004 five. The individual composition of these assemblies was never the same, although some animals were seen together several times.

In 2002, seven coelacanths were found hovering in front of a U-shaped niche adjacent to a well-developed cave in Jesser Canyon (cave 2) (Fig. 4). Most of these animals were fully exposed to ambient light. Some of them were maintaining a horizontal position over the sandy ground, and others were orientated head-down with their ventral surface against the cliff. Inside caves, coelacanths were sometimes found upside down, with their ventral surface near the cave roof, a position that is often adopted by cave-dwelling fish.

No obvious interactions between individual coelacanths or between coelacanths and other species were observed. Although caves are narrow and the fish often hovered close to each other inside the caves, the inhabitants rarely touch one another or contact the substrate. Casual contacts were of short duration and never caused a sudden retraction. The coelacanths did not show any reaction to the numerous other fish observed inside and in front of the caves. No attempt at feeding was observed although some of these fishes were of ideal prey size, considered as potential prey species and swimming close to

†In May 2005, a ROV was used to search for coelacanths in Jesser, Diepgat, White Sands and Island Rock canyons. It revealed nine coelacanth encounters, all in Jesser Canyon. Five of the coelacanths observed were known individuals, two have not been identified and two were new individuals, increasing the number of individually known coelacanths to 26 within the park.

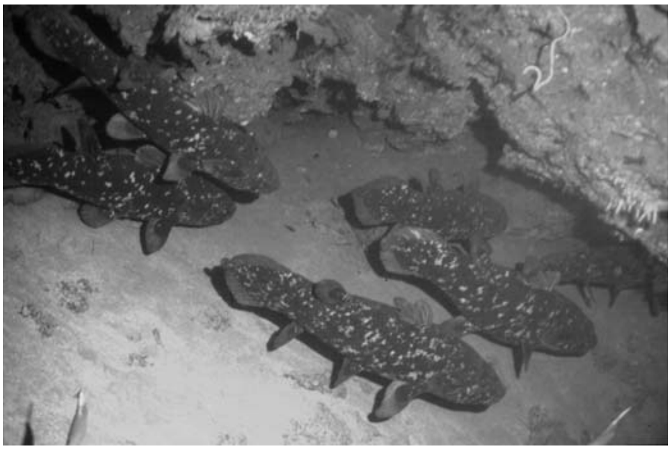

Fig. 4. Aggregation of seven coelacanths beside a submarine cave in Jesser Canyon at a depth of 111 m.

Fig. 5. Coelacanth individual 15 with ultrasonic transmitter attached.

the coelacanths' mouths (see Fig. 9b).

The coelacanths did not show any sudden reaction to the approach and presence of the submersible, although some individuals moved slowly deeper into the cave after being illuminated for filming. Occasionally, a coelacanth left the cave while it was under observation from the submersible. Video close-ups of the head region in the caves showed slow and small ventilation movements of the mouth and the operculum typical for the resting fish, which did not appear to be unduly perturbed. Coelacanths were filmed with both folded and unfolded first dorsal fin. Beside its locomotor function, the erection of the first dorsal fin might have a behavioural or motivational meaning such as lateral display.

Movements and acoustic tracking

During each of the three expeditions, several individuals were seen on numerous occasions, either in the same cave or at new localities. Thus coelacanths move between caves of which some are used regularly by different individuals. Individual 4, for example, was found in Jesser cave 2 during all of seven visits in 2003, and it was also found there on three times in 2002, indicating strong fidelity to the site. Some individuals were not seen for intervals of several days, suggesting that they were in caves that were not inspected during the survey period, or in caves not yet found. Two coelacanths encountered in Jesser were also seen in Wright, confirming that coelacanths move between these two adjacent canyons. None of the individuals documented in Chaka Canyon was seen in Jesser or Wright canyons, about 50 km north of Chaka (Table 3).

In 2003, a fish was tagged with an ultrasonic transmitter inside a cave at 133 m in Wright Canyon. It reacted to the penetration of the dart with a short forward acceleration but calmed down within seconds. The animal was re-sighted twice after tagging within a period of nine days. The tag was well seated and the fish appeared healthy and normal (Fig. 5). Tracking was accomplished on nine nights over a 17-day period. No full-night tracking (that is, from sunset to dawn) was achieved due to deteriorating weather and sea conditions. During the first three nights, the fish remained fairly stationary at around 106–111 m in the vicinity of a cave with an entrance that was too narrow to look inside. On the following nights, the fish was more active. Initiation and cessation of periods of activity varied and were not clearly linked to dawn and dusk. It roamed between 73 and 133 m, which was at, and shallower than, its daytime refuges at 96 and 133 m. While tagged, this fish was located at four different caves in two well-separated canyon arms. The distance between the two furthest caves was 2.5 km, measured along the 100-m depth contour line.

Scale sampling

Tissue samples taken from scales were required for population genetics, genome studies and stable isotope analysis. Genetic comparison with coelacanths from other locations should indicate whether the Sodwana examples form a distinct population, may provide hints of their derivation and information on the genetic variability within the colony.

A total of 15 scales were removed from six fish. As with the acoustic tagging, there were no apparent signs of serious stress nor any abnormal behaviour induced by scale sampling. All six coelacanths responded to the effect of the projectile with a short stroke of the caudal fin, resulting in a short forward movement; the fish then calmed down again within seconds. The position where the scale(s) are removed is usually visible as a lighter area (Fig. 6). Some of the sampled individuals were re-sighted several days after scale removal and the 'sampled area' was still evident; no adverse effects or infections were apparent. Two of the three animals from which scales were collected in 2002, were re-located in the same cave in 2003; one of them was seen also in 2004 (see Tables 2 and 3). The sampled areas were not evident, suggesting that the scales were already completely or partly regenerated.

The results of the genetic[22] and isotope analyses are presented elsewhere.

Environmental conditions

Surface water temperatures in April/May 2002–2004 off Sodwana had a mean of 26.2°C (range 24.4–26.9°C). Temperature remained relatively warm within the first 40 m, decreased more rapidly down to 70–80 m and then again less rapidly beyond that depth. Figure 7 gives an example of a typical temperature profile taken in Jesser Canyon. At 100 m, water temperatures inside or at the edge of the canyon ranged from 17.4 to 23.9°C (mean 19.2°C), and at 150 m, from 15.8 to 17.5°C (mean 16.7°C). Temperatures in Wright Canyon were similar, ranging at 100 m from 15.7 to 18.2°C (mean 17.8°C), with a mean of 16°C at 150 m, 15°C at 200 m, 13°C at 300 m and 12°C at 350 m. The temperature profiles of the other canyons were similar, with means of 18.8°C at 100 m and 16.3°C at 150 m. Highest values were measured in 2004, which apparently was a relatively warm year compared to 2002 and 2003.

In Jesser Canyon coelacanths were encountered at 16–22.5°C, in Wright at 16–19°C and in Chaka at 17–19.5°C. The most frequently occupied cave, Jesser cave 2, was inhabited by

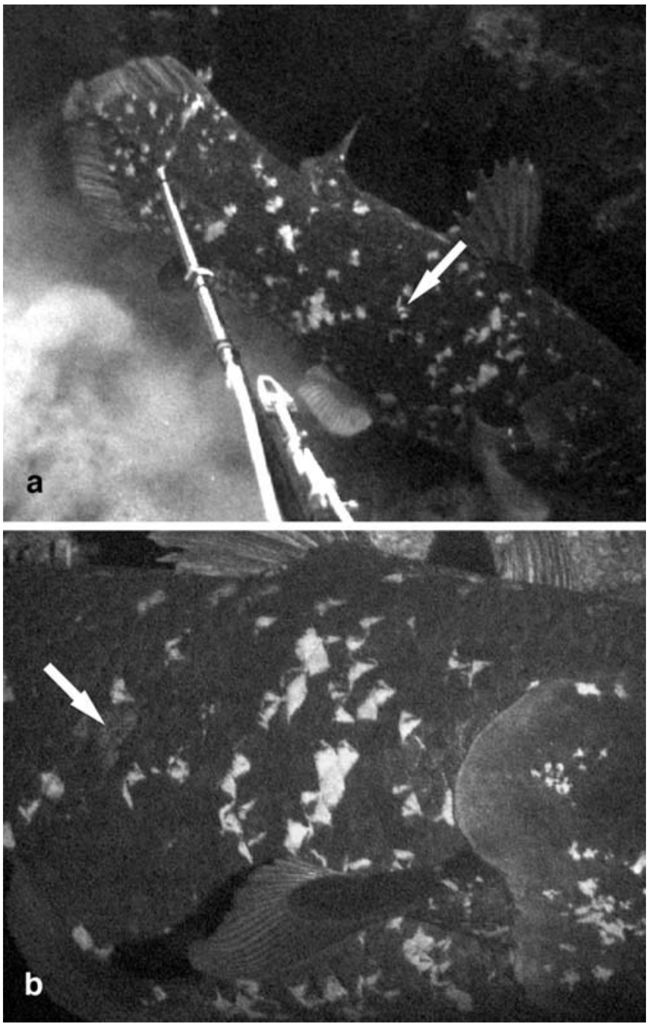

Fig. 6. Scale sampling on a coelacanth (individual 4) at a depth of 111 m, using a dart fired by an air gun attached to the submersible's manipulator arm. (**a**) Sampling projectile attached to fish (indicated by arrow); (**b**) sampled area, with two large scales removed, 17 days later.

coelacanths at 16–19°C in 2002 and 2003. In 2004 the cave was found to be empty at 20 and 22.5°C, whereas cave 3 at 125 m depth was occupied at 22.5°C, a relatively high value for this depth. Water temperature in caves that were occasionally occupied ranged from 16–22.5°C. No significant correlation between temperature and occupation rate was found; a cave that was found to be occupied on a certain day could be empty the next day while the temperature inside the cave remained the same.

The fish tagged in 2003 moved between depths of 70 and 130 m over a temperature range of 15–21°C.

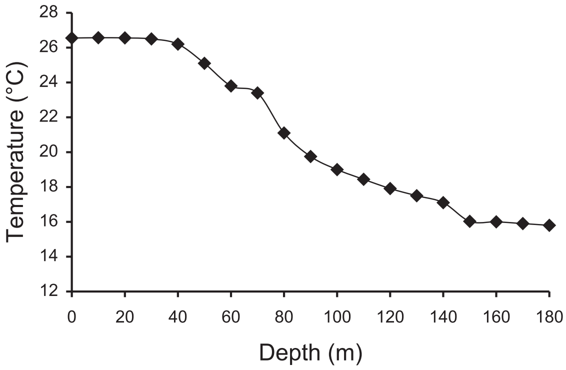

Fig. 7. Temperature profile taken in Jesser Canyon by CTD device attached to the submersible on 19 April 2003.

The minimum dissolved oxygen concentration was found between 110 and 140 m. This means that Sodwana coelacanths live slightly above or within the oxygen minimum layer.

Ambient light intensity was not measured, but it was sufficient to film the canyon habitat and the fish with a low light intensity camera and to manoeuvre the submersible without additional light at the depths at which coelacanths live.

The surface current off Sodwana measured in April–May was usually strong and regularly 2–3 knots (100–150 cm s^{-1}), north to south. During most dives, the current slowed down within the first 50–60 m depth and became weak or was absent when reaching the seabed close to the canyon edges. The sandy substrate on the plateau that surrounds the canyon heads was often covered by a layer of organic material (detritus, biofilm) that would not settle in continuously strong currents. Ripple marks and sand dunes were also found on the shelf plateau, which are clear indications of bottom currents, especially in areas shallower than 80 m depth.

There were almost no currents inside the canyons. Ledges and protuberances along the canyon walls were often covered by fine silt. On steep cliffs below 160 m, branched glass sponges (genus *Sclerothamnus*), which are extremely fragile and easily break off in areas exposed to currents, were frequently found. At times weak up- and downwellings were noticed. Inside the canyons, particularly along the canyon floor (thalweg) at depths of 200–350 m, there were again ripple marks and sand dunes, but also stagnant areas creating traps for different materials like flotsam and detached benthic organisms. During one dive a small vortex, like a 'dust devil', was seen moving along the canyon floor.

The visibility within the canyons was usually good (more than 10 m) and did not impose visual restrictions on surveys. An exception was Leven Canyon, which was inspected twice. The water was clear in the vicinity of the canyon and in depths shallower than 60 m, but the visibility suddenly became extremely bad on descent into the canyon and did not improve with depth.

Off Sodwana, the density and diversity of fish observed at the edge of the canyons and even inside the caves was surprisingly high (Fig. 8). Many fish species in the GSLWP coelacanth habitat can be considered as possible prey for coelacanths. A detailed report on the fish communities of the Sodwana canyons and their surroundings is given in this issue.[19]

Discussion

The priority research focus of the submersible surveys within and around the canyons off Sodwana Bay was to determine the population size and distribution of coelacanths in the GSLWP. However, coelacanths are cave-dwelling fish that cannot be counted with conventional stock assessment methods. Their daytime refuges must be found visually. Searching for coelacanths in a highly structured habitat with canyon margins of more than 100 km length and caves that penetrate deep into the slopes is therefore very time-consuming. Dive time was limited by funds, weather and ship schedule. After many hours spent searching underwater and scanning most of the suitable habitat at depths between 100 and 130 m, 24 coelacanths were found in only three of the 12 main canyons examined. It is assumed therefore that the entire population off Sodwana is not large and that not all canyons that have been mapped in the vicinity are inhabited. Coelacanths are apparently not abundant within the boundaries of the park, and *Latimeria* cannot be considered a common and widespread fish species in this area. Since at least two of the sighted coelacanths were most likely pregnant females,

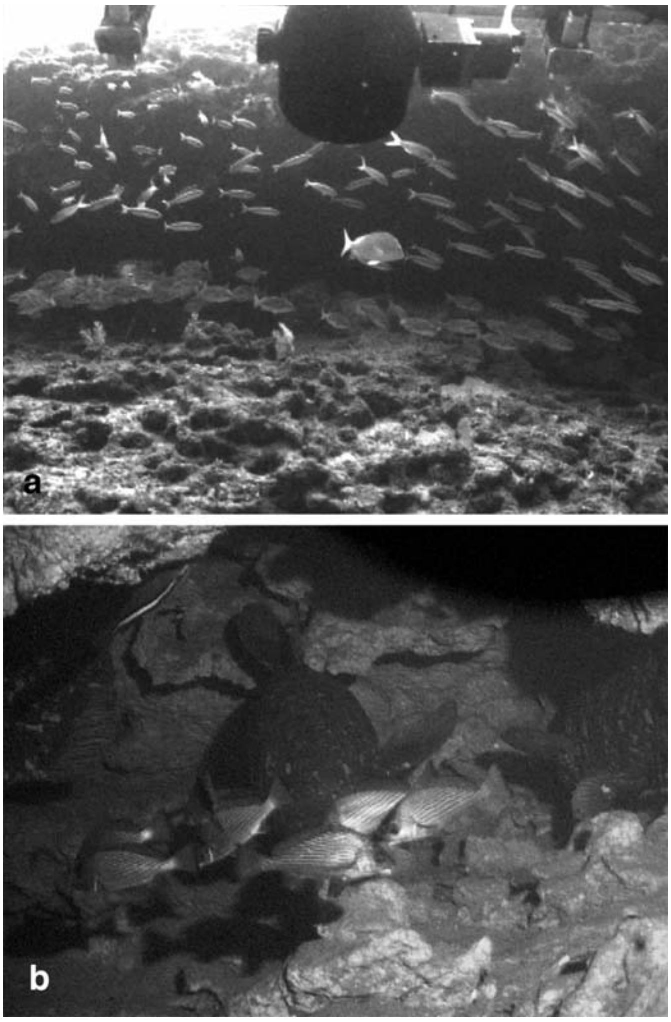

Fig. 8. (**a**) Low light camera image of fish density at canyon edge, and (**b**) school of fish inside coelacanth cave.

we assume that this colony is a viable breeding population.

A single dive per canyon, or dives that cover only sections of a canyon, are not sufficient to establish whether coelacanths are present in any particular canyon. From cave inspections, coelacanths were found to change caves, and those caves that were known as regular coelacanth rest sites (such as Jesser cave 2) were not always occupied. In a huge canyon, such as Wright, which has several branches, there must be more suitable caves than those located so far. This is, for example, indicated by animals that were seen only once or with interruptions of several days during the course of a cruise. They might have used caves that were either not regularly inspected or not yet found.

During each cruise animals were encountered that had not been seen before; the number of new sightings was still slightly higher than the number of animals re-sighted within the last four years. Thus, the entire coelacanth population and habitat are not yet fully explored. Nevertheless, we believe that the coelacanth colony within the GSLWP consists of a relatively small number of resident animals. Jesser Canyon seems to be a kind of nodal point with the highest number of coelacanth sightings in relation to the number of dives per canyon. This number was lower in the neighbouring large canyon (Wright), although several shelters were found there that appeared to be suitable for coelacanths. Most of these well-spread sightings in Wright Canyon were encounters with single individuals although some of the caves inspected were huge and could accommodate many animals. Aggregations of more than two individuals were found only in Jesser and once in Chaka canyons. The largest number of animals seen together was seven. At the Comoros, in comparison, assemblies of up to 16 animals in a cave not much larger than cave 2 in Jesser have been documented. It is conceivable that the coelacanth habitat off Sodwana is under-populated, its carrying capacity, in terms of suitable caves and protected sites for *Latimeria* not yet being fully exploited.

Present data and understanding of the physical and ecological environmental requirements of coelacanths do not provide any hint that could explain why canyons like Leadsman South or Mabibi, with at least some suitable shelters and sufficient prey abundance, are apparently not, or not regularly, occupied. No physical factors were detected that would make potentially suitable caves less or more attractive for coelacanths than others. Temperature recordings inside the caves, for example, did not fluctuate to an extent that could be used to explain differences in occupation rates. Some of the Sodwana canyons, however, seem to be unsuitable or less suitable for coelacanths due to a lack of suitable shelters, at least in those depths where coelacanths were found in Jesser, Wright and Chaka canyons. Leven Canyon has large caves, especially around 120 m, but this canyon was extremely turbid and the apparent absence of coelacanths here may be related to this high turbidity. The silt might have been raised by water moved by the tides up and down the canyon floor, but this does not explain why such poor visibility was restricted to Leven Canyon.

Finding coelacanths in Chaka Canyon extended the linear distribution of coelacanths in the GSLWP to 53 km, with Chaka as the southern and Wright as the northern boundary. Preliminary sonar surveys several kilometres south of Chaka revealed no further canyons or structures comparable in dimension to those off Sodwana Bay.

A single coelacanth was photographed by divers at a depth of 54 m below an overhang in a deep reef complex on the shelf south of Diepgat Canyon (C. van Jaarsveld, pers. comm. 2004). The fish had not been sighted before. This exceptional find represents the shallowest documented sighting of a coelacanth. The water temperature was 17–19°C. Although a single observation, it suggests other habitats that supply sufficient shelter for coelacanths might be inhabited, either regularly or occasionally if the conditions (temperature and currents) are conducive. Time constraints unfortunately prevented exploration of the scattered deep reef complexes within the park. The find is also surprising since no coelacanths were found in Diepgat Canyon, which is 10 km south of Jesser and 37 km north of Chaka.

Coelacanth behaviour

This study confirms that, like their Comoran and Indonesian counterparts, South African coelacanths use submarine caves as resting sites in which they sometimes gather during daytime. Several animals share the same home range and obviously prefer the same caves. However, it is not known why. Clustering of organisms can be a consequence of social behaviour, or a response of individuals to environmental cues. It is possible that different individuals use the same caves regularly because they are the most suitable shelters. In this case there would be no social background for gathering and aggregations would occur more or less coincidentally, depending on which cave is approached by the single fish after searching for prey on its own. Single animals were found relatively frequently, particularly in caves at Wright Canyon as mentioned above.

Coelacanths tolerate their own kind. So far, however, there are no indications that coelacanths are social, in that they live in groups in which members maintain different relationships from other individuals. The individual membership of the aggregations changes; some animals were seen together several times but were not continuously grouped. It is possible that individuals recognize each other, but no interactions that corroborate this hypothesis have been observed. No antagonistic behaviour has been observed, even when the fish almost touch each other inside a cave. It would be premature to consider such coelacanth assemblies as social or even family groups.

Aggregations do not seem to be a seasonal event. The discovery divers saw three animals together in Jesser cave 2 in October and November 2000[7] and this study observed an aggregation of seven animals at the same location in April 2002, suggesting that coelacanths may collect at different times of the year if not throughout the entire year.

Coelacanths did not show a significant reaction to the presence of the submersible, unlike some other fish that may flee or disperse when suddenly illuminated or if the submersible's keel touches rocky substrate and produces a scraping noise. Low light intensity cameras as well as cameras in combination with artificial light were used, but significant differences in the behaviour of the coelacanths being filmed were not observed. It seems as if the submersible, its lights, the sound of its motors and the occasional ultrasonic underwater communication do not disturb these fish.

Movements and tracking

Tracking coelacanths off the KwaZulu-Natal coast is not as easy as off the Comoros, where the sea is often very calm. Off Sodwana, surface-based tracking was usually restricted by strong wind and currents. Nevertheless, the first ultrasonic tracking experiment of a South African coelacanth revealed a preliminary insight into the nocturnal activities of the fish that might be typical for the coelacanths off Sodwana. Although also active at night, the tagged fish seemed to have a reduced activity period compared to the Comoran coelacanths. It spent at least some nights inside or close to a cave. The start and end of its movements were not restricted to a particular time as found for the Comoran fish. Foraging movements of Comoran coelacanths usually started shortly after sunset and ended before sunrise.[18]

The tagged Sodwana coelacanth moved in depths between 73 and 133 m, mostly at or above the depth of its daytime refuges (96–133 m). Comoran coelacanths, in contrast, are most active between 200 and 300 m, which is below their resting depth at 160–250 m. Especially large fish regularly perform excursions down to 400 m and deeper, with the deepest record at almost 700 m.[18] The 60 m vertical activity range of the Sodwana fish was less than most Comoran coelacanths, which regularly traverse 100–500 m depth ranges. The absence of a deep-water excursion in the Sodwana fish likely reflects responses to different circumstances in South Africa and the Comoros. In South Africa, the density of potential prey fish was found to be high at and slightly above the depth of the coelacanths' daytime refuges, and water temperatures measured at these depths are within the supposed preferred temperature range of the fish (see below). The coelacanth caves off Grand Comoro are located in a depth range where prey abundance is generally low; fish counts at and below cave level down to 400 m revealed an increase in abundance with depth of bentho-pelagic and mainly nocturnally active prey species that were also found in the stomach of caught coelacanths.[12] The tagged Comoran coelacanths spent most of their active time in temperatures of 15–19°C and rarely ventured into waters warmer than 22°C measured at depths shallower than 160 m.[18] They obviously avoid shallower warmer waters where they would probably suffer hypoxic stress (see below). Prey abundance and water temperature probably shape the different patterns of vertical movements in coelacanths off Sodwana and Grand Comoro. Unlike their Comoran relatives, Sodwana coelacanths do not need to move into deep water to find prey, as potential prey is abundant and temperatures are comfortable at the depths of their daytime refuges.

Coelacanths are slow moving fish that restrict their activities to relatively small areas. The tagged fish at the Comoros usually stayed in an area of less than a kilometre in radius around their resting sites, rarely moving more than 3–4 km per night.[18] The largest linear distance measured between the two furthest positions of a tagged fish obtained throughout its entire tracking period of two days was 11 km. The tagged Sodwana coelacanth stayed in a relatively restricted area in which it used different caves. On some nights the tagged fish seemed to restrict its movements to small excursions around its daytime refuge; on other nights, it moved several hundred metres along the canyon margins. Although it stayed in the same canyon whilst being tracked, it was found in two different arms of the canyon separated by more than 2 km. From re-sightings of two fish in both Jesser and Wright canyons, we know that the Sodwana coelacanths move between canyons, but not how often and to what extent. Further tracking experiments with data-storing receivers moored on the seabed between canyons should provide this information. Preliminary experiments to test the practicability of this method in highly structured areas were conducted in 2004 with *Jago* carrying an ultrasonic tag. Coelacanths do not appear to move long distances, as suggested by their strong site fidelity and the fact that at the Comoros and Sodwana no migrants were found at dive sites separated by more than 35 km.

The oceanographic measurements taken with *Jago* inside or at the entrance of the coelacanth caves provide the first on-site information on the physical conditions within the coelacanth habitat at Sodwana Bay. They revealed that the physical environmental conditions under which coelacanths live off Sodwana are similar to those off the Comoros, although South African coelacanths inhabit caves that are about 100 m shallower than at the islands and are therefore more exposed to light. More light could, for example, favour visual prey detection, at least during the day. Coelacanth eyes are well adapted to low light conditions,[23] and it is possible that the Sodwana coelacanths feed at any time on the numerous fish that occur inside and in front of their caves. At night and in complete darkness, other senses like electroperception[24] are probably used by coelacanths for prey detection.

At both locations coelacanths live within the same temperature range and in habitats that are not regularly exposed to strong currents, at least inside the canyons. As sluggish fish, coelacanths appear to avoid strong currents. The Sodwana canyons seem to provide ideal shelter. Even on the shelf surrounding the canyon heads, bottom currents were not as strong as expected; the strong surface currents, part of the fast-flowing Agulhas Current system, decrease within the first 50 metres, probably the result of friction between the water masses and the seabed. This situation is also favourable for migrations between canyons for which the fish have to cross a sandy plain without sheltering structures. It is, however, possible that these occasional crossings take place only on nights where bottom currents are absent or extremely weak.

It is assumed that coelacanths prefer certain temperatures because of their blood physiology and gill morphology.[25,26] Coelacanths have a small gill surface area in relation to body size and therefore a low oxygen diffusing capacity. This is apparently compensated with a high oxygen affinity of their haemoglobin that is most effective at temperatures between 15–20°C, which corresponds to the temperature range in which coelacanths are most frequently found in Sodwana and the Comoros. Warm water increases the metabolic rate and therefore oxygen demand, and consequently, the respiratory activities of the fish, an effect compounded by the reduced oxygen content of warm water. Temperatures higher than 20°C could cause respiratory distress and should therefore be avoided by coelacanths. Two live Indonesian coelacanths (*Latimeria menadoensis*), which were observed in a cave at 155 m off North Sulawesi, were also found within this temperature range.[14] Off Grand Comoro, however, temperatures of up to 24–25°C in occupied caves were measured on occasion,[27] values that clearly lie above the upper end of the range. This suggests that, at least during resting and presumably at correspondingly low metabolic rates, coelacanths are probably more tolerant of higher temperatures than previously assumed. The Sodwana coelacanths already have shown that they can tolerate a temperature range of 7°C.

Since their discovery off Sodwana in 2000, additional coelacanths have been found at other locations along the East African coast.[6] The study in South Africa shows that coelacanths can survive in areas that are known to be influenced by strong currents if calmer waters and sufficient shelter are available in deeper zones. Submarine canyons of similar dimensions have been found off Mozambique, Tanzania and Madagascar. It is possible that coelacanths live in scattered groups along these locations in the same manner as they live in their caves off South Africa, the Comoros and Indonesia.

The participation of the German team in the African Coelacanth Ecosystem Programme was supported by the Federal German Ministry of Education and Research (BMBF) and the Max Planck Society (MPG). At the BMBF we especially would like to thank Christian Manthey (International Büro) and Peter Wenzel-Constabel for their efforts, at the MPG Berthold Neizert. Funds were also provided by the German Research Council (grants FR 369/20-1 and 445 SUA-113/11/0-1). The National Research Foundation, the Department of Science and Technology and the Department of Environmental Affairs and Tourism are the main supporters of the programme in South Africa. We are particularly indebted to the captains and crew of the research vessel FRS *Algoa* for the safe handling of the submersible in sometimes difficult sea conditions. We experienced excellent support for the launch and recovery of the sub by the MCM team of Mike Roberts, Marcel van den Berg, Tammy Morris, Niel Engelbrecht, Rick Harding and Rex Quick. Many thanks also to James Stapley and Rosie Dorrington. The telemetry experiment would not have been possible without the help of the skilful Sodwana divers Peter Timm and his friends Willem de Beer, Grant Brockbank, Rupert Cornelius, Frik Bal, Rob Bester, Wayne Schick and Buks. Ian Calvert at Smit Marine South Africa (Ltd) always had an open ear for our enquiries concerning the ship and its modifications for our purposes. We thank the Greater St Lucia Wetland Park Authority and project coordinators of Ezemvelo KwaZulu-Natal Wildlife for diving permissions and their staff for logistical support on site off Sodwana Bay.

1. Smith J.L.B. (1939). A living fish of the Mesozoic type. *Nature* **143**, 455–456.
2. Bruton M.N., Cabral A.J.P. and Fricke H. (1992). First capture of a coelacanth *Latimeria chalumnae* (Pisces, Latimeridae), off Mozambique. *S. Afr. J. Sci.* **88**, 225–227.
3. Heemstra P.C., Freemann A.L.J., Yan Wong H., Hensley D.A. and Rabesandratana H.D. (1996). First authentic capture of a coelacanth, *Latimeria chalumnae* (Pisces, Latimeriidae) off Madagascar. *S. Afr. J. Sci.* **88**, 225–227.
4. Schliewen U., Fricke H., Schartl M., Epplen J.T. and Pääbo S. (1993). Which home for coelacanths? *Nature* **363**, 405.
5. De Vos L. and Oyugi D. (2002). First capture of a coelacanth, *Latimeria chalumnae* Smith, 1939 (Pisces: Latimeriidae), off Kenya. *S. Afr. J. Sci.* **98**, 345–347.
6. Benno B., Verheij E., Stapley J., Rumisha C., Ngatunga B., Abdallah A. and Kalombo H. (2006). Coelacanth (*Latimeria chalumnae* Smith, 1939) discoveries and conservation in Tanzania. *S. Afr. J. Sci.* **102**, 486–490.
7. Venter P., Timm P., Gunn G., le Roux E., Serfontein C., Smith P., Smith E., Bensch M., Harding D. and Heemstra P. (2000). Discovery of a viable population of coelacanths (*Latimeria chalumnae* Smith, 1939) at Sodwana Bay, South Africa. *S. Afr. J. Sci.* **96**, 567–568.
8. Lutjeharms J.R.E., Monterio P.M.S., Tyson P.D. and Obura D. (2001). The oceans around Southern Africa and regional effects of global change. *S. Afr. J. Sci.* **97**, 119–130.
9. Fricke H. and Plante R. (1988). Habitat requirements of the living coelacanth *Latimeria chalumnae* at Grande Comore, Indian Ocean. *Naturwissenschaften* **75**, 149–151.
10. Fricke H., Hissmann K., Schauer J., Reinicke O., Kasang L. and Plante R. (1991). Habitat and population size of the coelacanth *Latimeria chalumnae* at Grand Comoro. *Environ. Biol. Fishes* **32**, 287–300.
11. Fricke H., Schauer J., Hissmann K., Kasang L. and Plante R. (1991). Coelacanth *Latimeria chalumnae* aggregates in caves: first observations on their resting habitat and social behaviour. *Environ. Biol. Fishes* **32**, 281–285.
12. Fricke H. and Hissmann K. (1994). Home range and migration of the living coelacanth. *Mar. Biol.* **120**, 171–180.
13. Fricke H., and Hissmann K. (2002). Feeding ecology and survival of the living coelacanth. *Mar. Biol.* **136**, 379–386.
14. Fricke H., Hissmann K., Schauer J., Erdmann M., Moosa M.K. and Plante R. (2000). Biogeography of the Indonesian coelacanths. *Nature* **403**, 38.
15. World Conservation Union (1996). IUCN Red List of Threatened Animals. Gland, Switzerland.
16. Ramsay P.J. and Miller W.R. (2006). Marine geophysical technology used to define coelacanth habitats on the KwaZulu-Natal shelf, South Africa. *S. Afr. J. Sci.* **102**, 427–434.
17. Schauer J., Hissmann K. and Fricke H. (1997). A method for deployment of externally attached sonic fish tags from a manned submersible and their effects on coelacanths. *Mar. Biol.* **128**, 359–362.
18. Hissmann K., Fricke H. and Schauer J. (2000). Patterns of time and space utilisation in coelacanths (*Latimeria chalumnae*) determined by ultrasonic telemetry. *Mar. Biol.* **136**, 943–952.
19. Heemstra P.C., Fricke H., Hissmann, K., Schauer J., Smale M. and Sink K. (2006) Interactions of fishes with particular reference to coelacanths in the canyons at Sodwana Bay and the St Lucia Marine Protected Area of South Africa. *S. Afr. J. Sci.* **102**, 461–465.
20. Sink K., Boshoff W., Samaai T., Timm P.G. and Kerwath S.E. (2005). Observations of the habitats and biodiversity of the submarine canyons at Sodwana Bay. *S. Afr. J. Sci.* **102**, 466–474.
21. Bruton M.N. and Armstrong M.J. (1991). The demography of the coelacanth *Latimeria chalumnae. Environ. Biol. Fishes* **32**, 301–311.
22. Schartl M., Hornung U., Hissmann K., Schauer J. and Fricke H. (2005). Relatedness among east African coelacanths. *Nature* **435**, 901.
23. Locket N.A. (1980). Some advances in coelacanth biology. *Proc. R. Soc. B* **208**, 265–307.
24. Northcutt R.G. (1980). Anatomical evidence of electroperception in the coelacanth *Latimeria chalumnae. Zbl. Vet. Med. C. Anat. Histol. Embryol.* **9**, 289–295.
25. Hughes G.M. (1995). The gills of the coelacanth, *Latimeria chalumnae,* a study in relation to body size. *Phil. Trans. R. Soc. Lond.* **347**, 427–438.
26. Hughes G.M. and Itazawa Y. (1972). The effect of temperature on the respiratory function of coelacanth blood. *Experientia* **18**, 1247.
27. Hissmann K., Fricke H. and Schauer J. (1998). Population monitoring of the coelacanth (*Latimeria chalumnae*). *Conserv. Biol.* **12**, 759–765.

Unpublished reports

1. Hissmann K., Fricke H. and Schauer J. (2002). The South African coelacanth habitat – geomorphology and distribution of caves. ACEP Report, SAIAB, Grahamstown.
2. Hissmann K., Fricke H. and Schauer J. (2002). Megabenthos (invertebrates) biodiversity of the Sodwana Canyons – preliminary report. ACEP Report, SAIAB, Grahamstown.