Oceanographic environment of the Sodwana Bay coelacanths (*Latimeria chalumnae*), South Africa

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Trimix scuba divers discovered coelacanths in Jesser Canyon at a depth of 104 m on the northern KwaZulu-Natal (KZN) coast (Sodwana Bay) in October 2000. The existence of these animals at such a shallow depth and in the swift and powerful Agulhas Current led to a suggestion that this might be an isolated group swept well away from the main population in the Comoros, where they live at depths of 200–350 m with little current. Subsequent observations from three manned submersible surveys and one remotely operated vehicle expedition together with recreational diver observations indicate that the South African population of coelacanths has at least 26 individuals, mostly occupying the depth range of 104–140 m in canyons. Seventeen CTD sections collected during four cruises in 2002 and 2003 indicate the temperature range in this habitat to be similar to that found in the Comoros Islands (that is, 15–22°C cf. 15–19°C in the Comoros). However, a 2.5-month-long time series of hourly data collected by a thermistor array deployed near a known coelacanth cave in Wright Canyon indicated greater variation than anticipated, with temperature changes between 16°C and 24°C occurring in a day. Dissolved oxygen levels in this depth zone were found to range between 3.0 ml l^{-1} and 4.8 ml l^{-1} compared to 3.5 ml l^{-1} in the Comoros. The low oxygen values along this coast are a result of the shallow oxygen minimum, which becomes shallower in the southwest Indian Ocean, particularly in the Agulhas Current, than in tropical latitudes. Current velocities measured using a ship-borne ADCP in the depth range 100–140 m at Sodwana were considerably higher than those measured in the Comoros habitat (20–60 cm s^{-1} cf. 3–4 cm s^{-1}) and may be an important factor explaining the coelacanths' occupation of the canyons found along the northern KZN shelf-break.

Introduction

The discovery in October 2000 of three coelacanths by Trimix scuba divers at a depth of 104 m in Jesser Canyon[1] (Fig. 1b) on the northern KwaZulu-Natal (Maputaland, KZN) coast, South Africa, caused much excitement in scientific circles. Twenty-six coelacanths have been identified using scuba, a remotely operated vehicle (ROV) and a manned submersible (*Jago*). They were seen in or close to Jesser, Wright and Leven canyons at depths between 104 and 140 m.[2] One individual was also found and photographed by scuba divers near the shelf edge at a depth of 54 m below an overhang at a reef a little south of the mature Diepgat Canyon. This exceptional find is the shallowest documented sighting of a coelacanth.[2] Coelacanths have not been found in the 17 other canyons of this region.[3] Coelacanths of the Comoros live at depths between 200 and 300 m.[4]

The Maputaland shelf is shallow relative to the rest of South Africa and is mainly sandy with dispersed coral reefs.[5,6] The shelf-break between Cape St Lucia and Inhaca Island occurs at an approximate depth of 50 m, with the slope dropping sharply to 1000 m into the upper reaches of the Natal Valley.[7] The steep heads of the canyons tend to be stratified and rocky with occasional substantial cliffs and intermittent sandy terraces providing overhangs and caves, which might be suitable refuges for coelacanths.

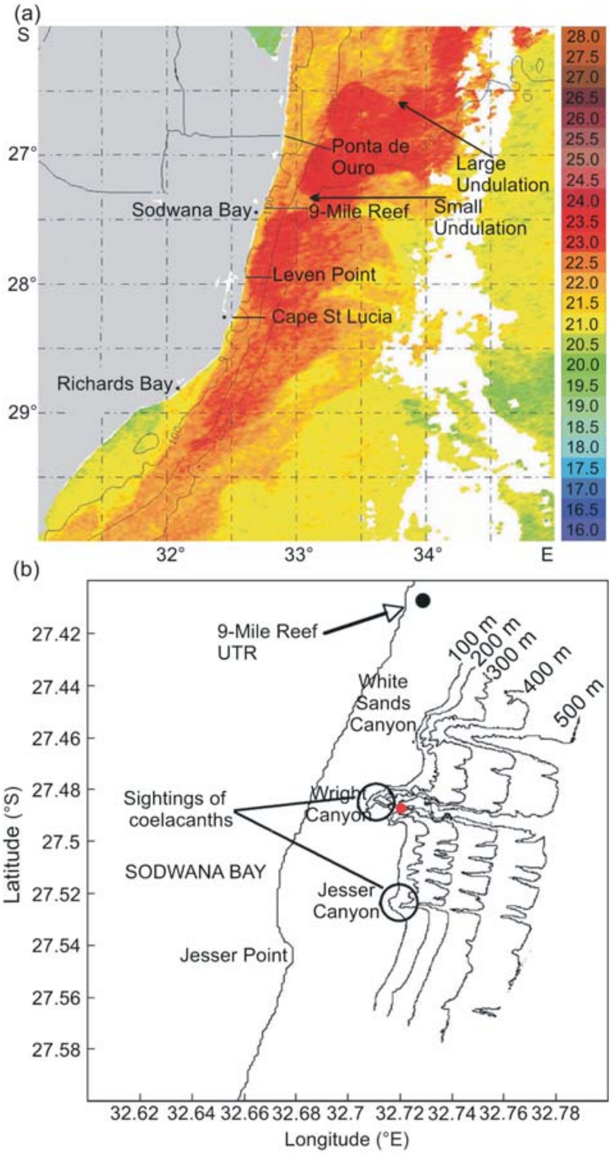

Fig. 1. (**a**) SST image on 17 July 2003 shows the core of the Agulhas Current (red) approaching the Maputaland shelf north of Ponta do Ouro. The current moves away from the coast south of Cape St Lucia. Positions of CTD transects stipulated in Table 1 are depicted. Scale in °C. (**b**) Bathymetry near Sodwana Bay highlights the positions of Jesser, Wright and White Sands canyons. The position of the thermistor array is also shown (red dot) in a side valley of Wright Canyon.

Coelacanths are predatory fish which are drift hunters.[8] Acoustic telemetry studies and video analysis estimate very slow average swimming speeds of *c.* 5 cm s^{-1}, which, according to a study in the Comoros,[4] is compatible with the weak currents measured in their habitat. It was unexpected therefore that they would be in canyons of the narrow Maputaland shelf, which is

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Table 1. Summary of maximum and minimum temperatures (*T*) and dissolved oxygen concentrations between 100 m and 140 m at Sodwana Bay (data from four cruises).

Date	Area	*T* at 100 m (°C)	*T* at 140 m (°C)	Oxygen at 100 m (ml l^{-1})	Oxygen at 140 m (ml l^{-1})
30 Mar 2002	Nine-Mile Reef	19	16	3.6	3.9
01 Apr 2002	Nine-Mile Reef	19	16	3.6	3.9
02 Apr 2002	Nine-Mile Reef	19	17	3.7	3.7
05 Apr 2002	Nine-Mile Reef	18	15	3.5	4.0
05 Apr 2002	Leven Point	18	16	–	–
09 Apr 2002	Nine-Mile Reef	19	16	3.7	3.8
12 Apr 2002	Nine-Mile Reef	21	18	–	–
14 Apr 2002	Nine-Mile Reef	20	17	3.8	3.7
16 Apr 2002	Nine-Mile Reef	20	18	3.6	3.3
31 Jul 2002	Ponto da Ouro	22	21	4.7	3.9
17 Aug 2002	Nine-Mile Reef	20	18	3.8	4.1
17 Aug 2002	Leven Point	20	19	–	–
03 May 2003	Ponto da Ouro	19	17	3.2	3.1
04 May 2003	Nine-Mile Reef	17	16	3.4	3.3
14 July 2003	Leven Point	21	18	3.1	3.0
14 July 2003	Nine-Mile Reef	21	19	3.2	3.0
15 July 2003	Ponto da Ouro	19	17	3.0	3.1
Mean		20	17	3.6	3.6
Max.		22	20	4.8	4.1
Min.		17	15	3.0	3.0

swept by the fast, warm Agulhas Current — one of the world's most powerful western boundary currents where surface velocities are in excess of 200 cm s^{-1}.[9] Figure 1a shows a sea-surface temperature (SST) satellite image of 17 July 2003, in which the Agulhas Current flows close to the shelf edge off Sodwana Bay until Cape St Lucia, which is known by mariners, divers and fishermen to strongly influence the narrow shelf environment. Divers on the adjacent inshore coral reefs commonly report strong southward-flowing currents. An acoustic Doppler current profiler (ADCP) deployed in 26 m near 9-Mile Reef confirms the existence of a dominant, strong, southward current which commonly reaches 0.5–0.75 m s^{-1} (M. Roberts, unpubl. data). Little in the way of oceanography, however, has been formally recorded in northern KwaZulu-Natal and so current velocities and the physical environment in this region are poorly understood.

Few measurements of the Agulhas Current itself exist and hence its behaviour in this region is also poorly understood. SST imagery indicates that the current occurs further offshore in the northerly region of the Delagoa Bight, but then shifts towards the coast somewhere near Ponta do Ouro, that is, 26°S. Lutjeharms[10] indicates that the Agulhas Current is only fully constituted around 28°S, in the vicinity of Sodwana Bay, and that the source of the current is complex and not a continuation of the 'Mozambique Current' as is so often portrayed in text books.[11] The 'Mozambique Current' in the form of a western boundary current in fact does not exist. Rather, flow in the channel is mainly via cyclonic and anticyclonic eddies,[12] which propagate southwards. The source of the Agulhas Current is therefore a confluence of flows from the Mozambique Channel and southern Madagascar, also in the form of cyclonic and anticyclonic eddies which propagate westwards, as well as the re-circulation of the South-West Indian Ocean subgyre.[9,12]

The data presented in this paper are among the first collected on the shelf edge in this region and were obtained during four multidisciplinary coelacanth research cruises aboard the FRS *Algoa* between April 2002 and August 2003, during which oceanographers endeavoured to define the coelacanth habitat at Sodwana Bay in terms of water temperature, dissolved oxygen, and currents.

These were compared with the Comoros, the home of the largest population of coelacanths studied.

Methods

Oceanographic data were collected using the FRS *Algoa* in April 2002 (cruise 107), August 2002 (cruise 112), May 2003 (cruise 119) and July 2003 (cruise 122), usually at night when submersible diving was halted. The conductivity, temperature and depth (CTD) data were collected using a Seabird SBE 911 with a coupled Seabird SBE 43 dissolved-oxygen sensor. The oxygen sensor was calibrated using water collected by Niskin bottles at standard depths and the levels of dissolved oxygen (DO) determined using the Winkler titration method.[13]

Velocity data were collected using a ship-mounted Teledyne RDI 150-kHz ADCP. This had a water column penetration depth of approximately 170 m from the surface. Ensembles using 4-m bins were averaged over 180 s. The first bin was at a depth of 8 m.

A thermistor array was deployed for 2.5 months between 3 May 2003 and 13 July 2003 in a side valley of Wright Canyon at a depth of 250 m (Fig. 1b: 27°29.77′ S; 32°43.41′ E). The position was close to a large cave in the precipitous canyon side-wall where two coelacanths had been observed at a depth of 135 m.[2] The array comprised 150 m nylon rope (diameter 10 mm) supported with floatation at the top and two Mini Benthos acoustic releases at the bottom for recovery. A pressure sensor was placed at the top of the array to monitor mooring tilt during strong currents. Individual (self-contained) Star-Oddi mini underwater temperature recorders (UTRs) with an accuracy of ±0.05°C were placed at depths of 95 m (top of array), 120 m, 145 m, 195 m and 245 m (2 m from the bottom). The hourly data are depicted in Fig. 5.

Inshore temperature data were collected by an UTR deployed on 9-Mile Reef at a depth of 18 m. This mooring has existed since March 1994. Data are downloaded every six months. Monthly averages for data between March 1994 and April 2005 are presented in Fig. 3. Daily averages for 2004 are shown in Fig. 5a and hourly data for February 2004 in Fig. 5b.

Results and discussion

Temperature

Between April 2002 and July 2003, 17 cross-shelf CTD transects of 40 km in length were collected variously at Ponta do Ouro, 9-Mile Reef and Leven Point (Fig. 1a); transect dates and a summary of the results are depicted in Table 1. As an example of the data collected, temperature and dissolved oxygen data for 9-Mile Reef collected on 14 July 2003 are shown in vertical sections to 1000 m in Fig. 2. A satellite image taken three days later on 17 July (Fig. 1a) highlights the behaviour of the Agulhas Current near this time (previous days had cloud cover). The SST signature of 23°C (maximum) indicates the core trajectory of the Agulhas Current to be offshore and away from the shelf north of 26.5°S. However, the current is seen to turn directly onshore at this latitude and to impinge on the shelf edge at Sodwana Bay (27.5°S), thereafter flowing close to the shelf edge southwards to Cape St Lucia. South of Cape St Lucia it moved away from the coast and followed the edge of the Tugela Bank. An undulation in the current boundary (perhaps trajectory) was present immediately north of Sodwana Bay. It is possible that the undulation observed in the SST image (Fig. 1a) was a little further north at the time the CTD line at 9-Mile Reef was undertaken and that the data presented in Fig. 2 represent the structure throughout the water column when the Agulhas Current is flowing firmly along the shelf-break. The *in situ* surface layer temperature was 22.8°C, which is closest to the value of 23°C measured in the remotely sensed data.

Surface temperatures in the CTD sections were found to range between 22°C in July/August and 26°C in March/April. Figure 2 shows that the greatest change in temperature occurs in the depth range 90–200 m. This means that the upper part of this gradient overlaps with the observed habitat of the coelacanth.

Measurements by an UTR positioned at a depth of 18 m further inshore on 9-Mile Reef showed inshore surface layer temperatures to be fairly representative of those offshore over the outer shelf and shelf-break (e.g. the surface layer in Fig. 2), and can be used to provide the expected seasonal variability of temperature in the surface layer in the immediate vicinity. The UTR data are shown in Fig. 3. The highest monthly mean temperatures occur in March, reaching 27°C; the lowest are experienced in August, with a monthly mean of 22°C. Hourly measurements (not shown), however, indicate that the surface temperature reaches a maximum of 28–29°C during summer with a minimum temperature of 17°C thought to be caused by some form of shelf edge upwelling. In the absence of upwelling, the minimum surface temperature in the record appears to be about 20°C. UTR data are corroborated by the CTD transects, which show lower surface temperatures between April and July, i.e. 22–23°C.

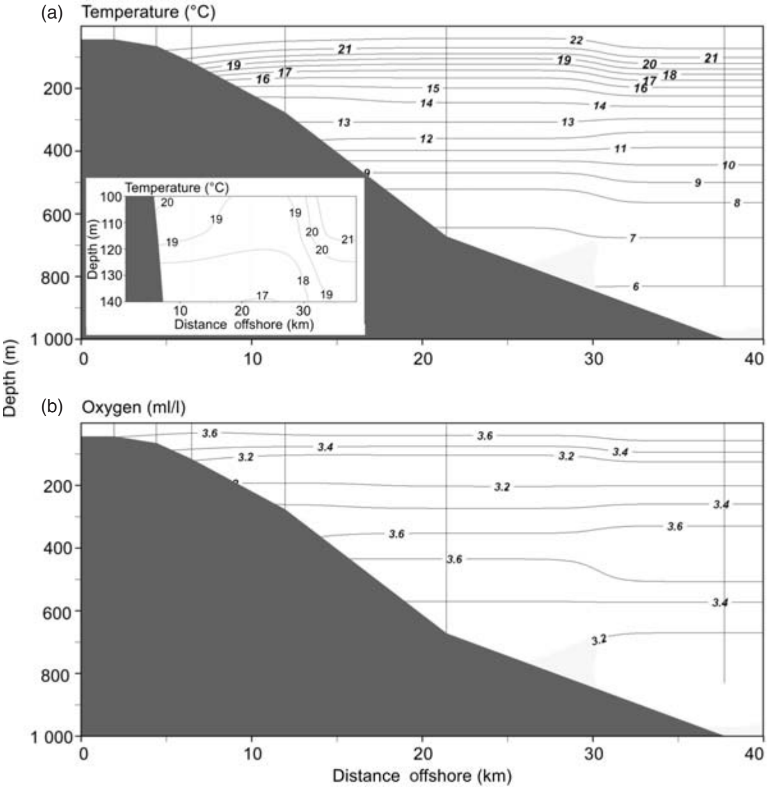

Fig. 2. CTD data collected along the 9-Mile Reef transect (see Fig. 1a for position) on 14 July 2003. (**a**) Vertical temperature (°C) to 1000 m with the depth range 100–140 m expanded (inset). (**b**) Vertical section to 1000 m of dissolved oxygen levels.

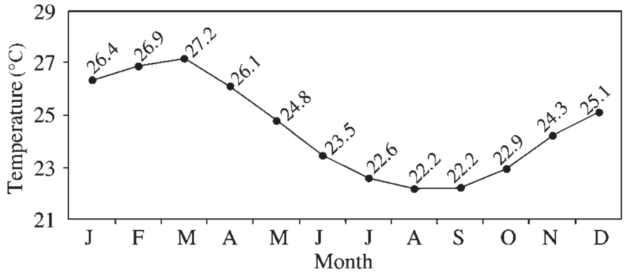

Fig. 3. Averaged monthly temperature data collected by an underwater temperature recorder (UTR) on 9-Mile Reef at a depth of 18 m. Hourly temperature data were used between March 1994 and April 2005.

A downward tilting of the isotherms was observed near the shelf break in several of the CTD sections. For example, the thermocline bends sharply downwards onto the shelf slope over a depth of some 100 m in Fig. 4a. One possible cause is shelf edge upwelling, which is observed in some of the vertical sections, e.g. Fig. 4b. Another could be downwelling over the shelf induced by strong southwesterly winds. This would force warm surface water down the slope. A similar situation has been observed on the Agulhas Bank off the Tsitsikamma coast (M. Roberts, unpubl. data).

Examination of the CTD data between the depths of 100 and 140 m (that is, the observed normal depths of the coelacanths) reveals a temperature range between *c.* 22°C at 100 m and *c.* 15°C at 140 m. These values were taken from expanded vertical sections such as in Fig. 2 (inset). The temperatures at these depths for each CTD transect are listed in Table 1. It is not known how this temperature range is affected by seasonal warming of the upper layer, especially in the Agulhas Current. Furthermore, there is no evidence of seasonal variability at 100 m in the CTD data listed in Table 1. According to these data, temperature at 100 m is slightly higher in the winter months. It should be noted that, because of the danger of losing the CTD in steep-sided canyons, no CTD dips were undertaken in the canyons, and therefore these observations may not necessarily be representative of the canyon environments.

The discovery of a coelacanth on 15 February 2004 at the shallow depth of 54 m on the shelf edge was most surprising, but the scuba divers reported the temperature on the bottom to be 17–19°C, which is well within the CTD measured range of 15–22°C for the depths of 100–140 m further down the shelf slope. Daily averaged bottom temperature data collected at 9-Mile Reef (see Fig. 1b) at a depth of 18 m for the year 2004 shows that the finding corresponds exactly with a significant upwelling event when the temperature fell from 27.3°C to 20.4°C. The hourly data set in Fig. 5b, however, shows the daily averaged data in Fig. 5a to be too smoothed and in fact the temperature on 15 February actually dropped to 17.8°C, which corresponds with the divers' observation. Scrutiny of the entire 9-Mile Reef UTR record (not shown) between 1994 and 2005 indicates that the 15 February upwelling event, in terms of the drop in temperature, is exceptional as is the other upwelling event later in December 2004 (Fig. 5a). The entire record shows that upwelling is not common along this coast, with a complete absence in some years.

The mechanism for the 15 February upwelling event can be seen in Fig. 6. (Note that 20 February was the first cloud-free day.) Ocean colour data in Fig. 6b show a plume of chlorophyll *a* stretching offshore for some 50 km. This is unusual since ordinarily the Agulhas Current is observed in satellite imagery to flow southwards parallel to the shelf edge past Cape St Lucia, and therefore would prevent such offshore advection. Moreover, upwelling and high chlorophyll *a* levels are not normally observed north of Cape St Lucia. Usually, the divergence of the Agulhas Current from the coast south of Cape St Lucia drives upwelling in the Natal Bight, as is seen in Fig. 6b by high chlorophyll *a* levels (orange–red colour).[14] The reason for the unusual offshore advection of chlorophyll *a* becomes clear in the altimetry data

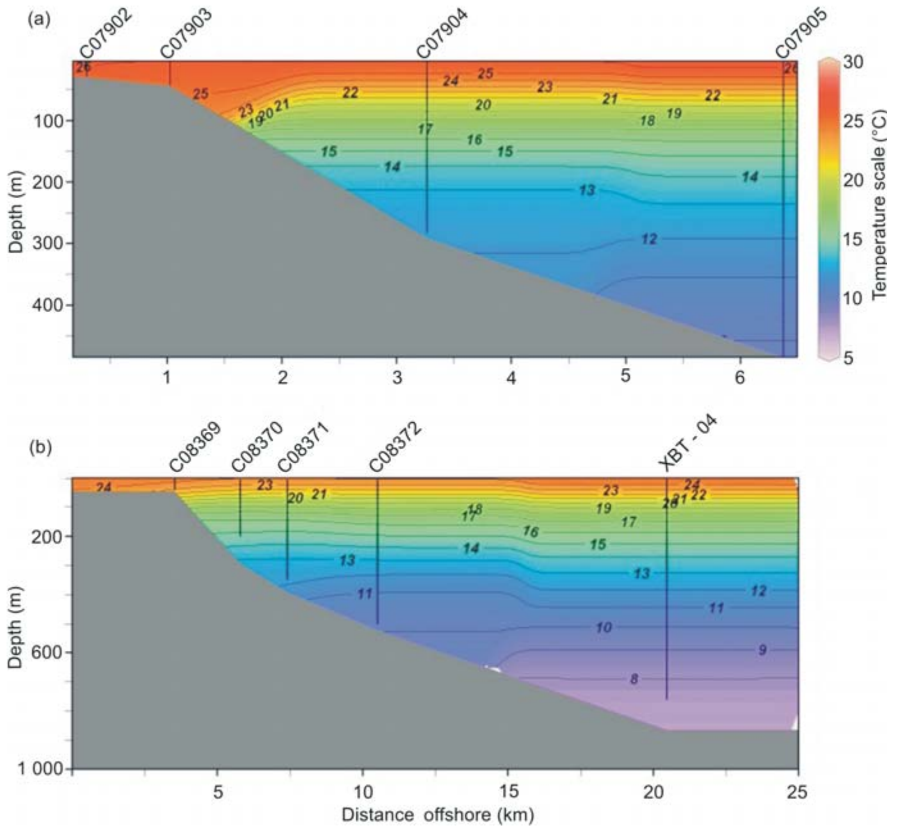

Fig. 4. Examples of isothermal structure of the water column off the Maputaland shelf. (**a**) CTD data collected on 5 April 2002 off 9-Mile Reef show the thermocline dipping down onto the slope. (**b**) CTD data collected on 4 May 2003 show shelf-edge upwelling.

shown in Fig. 6a. A meso-scale cyclonic eddy with a significant *c.* 30 cm depression in the sea-surface height (SSH) is observed just south of Cape St Lucia. The effects of this are to move the Agulhas Current offshore and around the outer periphery of the eddy as well as to pull inshore water away from the coast. This causes upwelling as demonstrated in the temperature records. Cyclones associated with the Agulhas Current are transient, moving southwards at speeds of *c.* 21 km/day.[15]

Clearly, the presence of a coelacanth at 54 m was exceptional. Whether coelacanths will move up the slope onto the shelf during more typical upwelling events remains to be seen.

It is intriguing that the Sodwana Bay coelacanths are found at such a shallow depth in South Africa compared with the Comoros. Temperatures measured in front of coelacanth caves

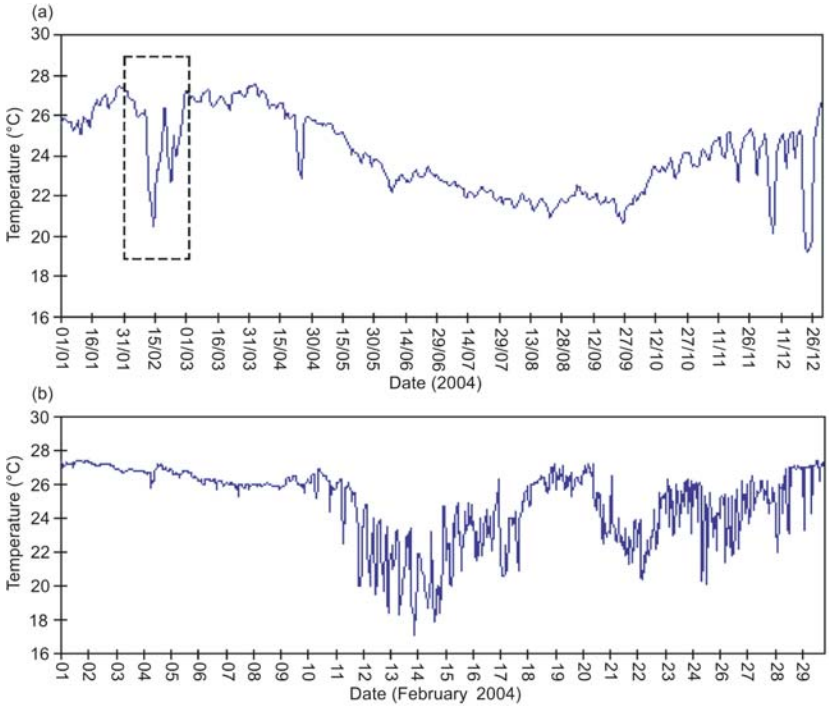

Fig. 5. (**a**) Daily averaged bottom temperature data collected at 9-Mile Reef (see Fig. 1b for location) at a depth of 18 m for the year 2004. The coelacanth found at 54 m on 15 February 2004 coincided with one of the most significant upwelling events between 1994 and 2005. (**b**) Expansion of February 2004 as an hourly data set shows the temperature on 15 February to have declined from 26.9°C to 17.8°C.

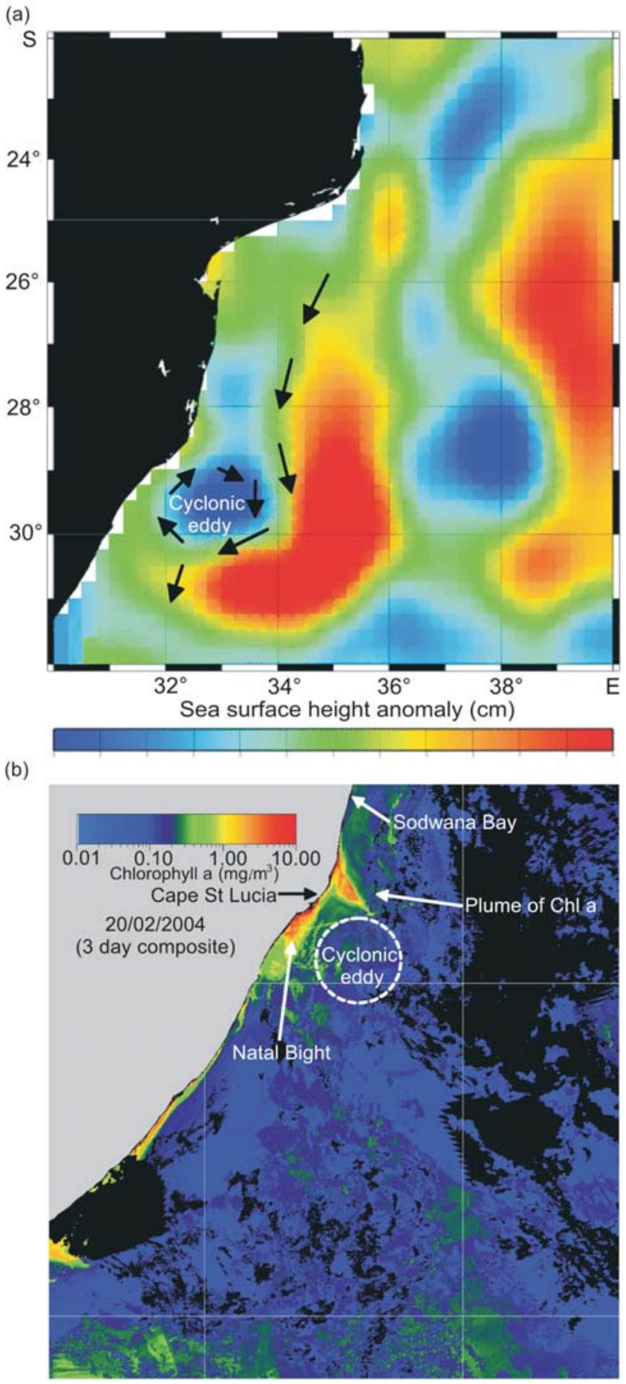

Fig. 6. (**a**) MODIS satellite sea-surface height anomaly data for 20 February 2004. The Agulhas Current has been moved away from the shelf by a cyclonic eddy positioned off the Natal Bight. (**b**) MODIS satellite ocean colour data for 20 February 2004. Note that the cyclonic eddy has induced shelf-edge upwelling and pulled a resultant plume of chlorophyll *a* offshore. The cyclonic eddy was responsible for the shelf-edge upwelling off Sodwana Bay on 15 February (temperature data in Fig. 5).

at the Comoros by the *Jago* team were found to range between 15.6 and 25.1°C[3,4] at depths of 200 and 350 m. Hissmann *et al.*[4] analysed the movement patterns of electronically tagged coelacanths and found that these animals spent 75% of their active time between 15 and 19°C, which corresponds closely with the temperature range for the Sodwana Bay coelacanths. It is difficult to detemine with confidence the respective roles of temperature tolerance and the need for shelter in prescribing the depth distribution of coelacanths.[16,17] Physical shelter, usually caves, seems to be essential during the day and so the presence or absence of shelter will affect distribution. Temperature tolerance and the physiological effects of temperature on metabolism also seem to affect depth distribution. The temperature range at the Comoros and Sodwana Bay in which coelacanth occur is essentially the same, but the caves at Sodwana are at a much shallower depth. Physiological studies of coelacanth metabolism and oxygen requirements[18] suggest that 15°C is the optimum temperature for the uptake of oxygen by coelacanth haemoglobin. At depths of 250–350 m off Sodwana the temperature range is much lower than the Comoros and is between 11–14°C. The fact that coelacanths have been found in a similar temperature range at both locations suggests that temperature tolerance affects the depth distribution of the fish.

The difference in the vertical temperature structure between Sodwana Bay and the Comoros is seen in the composite of four CTD transects in Fig. 7. As indicated on the map, the CTD stations were positioned along the shelf slopes of Africa and Madagascar and across the northern and southern parts of the Mozambique Channel to a depth of 500 m. The northern transect passes the Comoros (indicated in the figure). The apparent preferred temperature range of 15–19°C (green and yellow band in Fig. 7) at the Comoros is depicted between *c.* 200 and 270 m, and confirms that reported by Hissmann *et al.*[4] This range becomes shallower towards the south along the African continent, such that at Sodwana Bay it lies between *c.* 100 and 170 m. It is interesting that this temperature range is even deeper along the western shelf slope of Madagascar (i.e. *c.* 200–300 m). The southern trans-Mozambique Channel transect, as expected, shows an upward tilting of this temperature layer towards the west.

Temperature variability

The pressure sensor data collected at the top of the Wright Canyon thermistor mooring (with the exception of two data points which are erroneous) showed the array to have remained vertical throughout the deployment (Fig. 8a).

Results from the UTRs provide a longer-term perspective on the coelacanth environment, not captured in the CTD transect data. The time-series data for the period 3 May 2003 to 13 July 2003 for the five depths (Fig. 8b) reveal unusually rapid changes in the thermal environment, with an overall maximum temperature range of 13–24°C between 95 and 145 m, i.e. a *c.* 4°C broader range than measured by the CTD data. The mean temperatures for all five depths were 19.8°C (min. 14.6; max. 24.0; 95 m), 18.0°C (min. 13.5; max. 23.4; 120 m), 16.9°C (min. 13.3; max. 21.9; 145 m), 15.1°C (min. 11.0; max. 17.6; 195 m), and 13.8°C (min. 10.2; max. 16.5; 245 m). Two modes of variability are easily seen in the thermistor data — a high-frequency mode which appears at times to be tidally linked (discussed below), and a long periodicity ranging over a week or two, which is possibly linked to the behaviour of the Agulhas Current. The range of temperature fluctuations increases in the upper parts of the water column especially between 95 and 120 m.

In the first month of deployment (May) most of the variability of 2–3°C is observed in the 'tidal component' at all five depths, with the upper layers (i.e. 95 m, 120 m, 145 m) undergoing a gradual increase in the mean temperature from 16–18°C to 18–22°C. However, rapid cooling and heating in this habitat occurred in the first week of June, with the temperature at 95 m dropping from 24 to 17° C in a period of 2.5 days (event 1). This was followed by a period of 5 days where the temperature at 95 m oscillated rapidly between 18 and 23.5°C (event 2) while the temperature below 120 m was far more stable. The situation reversed two days later (event 3) for a similar period when the temperature at 95 m was stable but large fluctuations were experienced deeper at 120 m. A further two cooling events (events 4 and 5) separated by two days of large fluctuations followed. This high variability is seen only between 95 and 145 m,

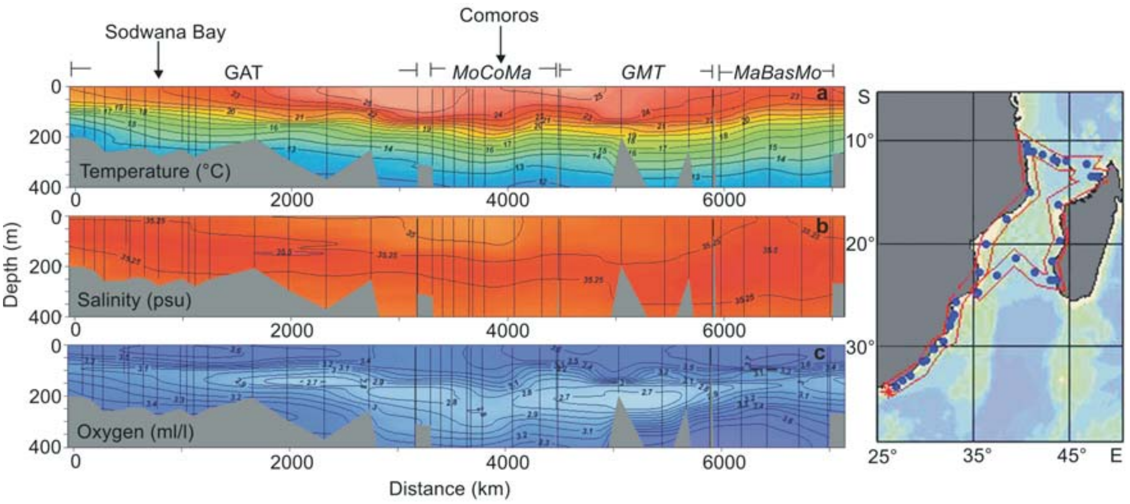

Fig. 7. Composites of CTD data collected along the East African shelf (GAT), across the northern Mozambique Channel (MoCoMa) past the Comoros, the west coast of Madagascar (GMT), and the southern Mozambique Channel (MaBasMo) (see map inset). (**a**) Temperature, (**b**) salinity, and (**c**) dissolved oxygen. Note the temperature range of 15–19°C (green and yellow band) and the SOM become shallower southwards towards Sodwana Bay relative to the tropics.

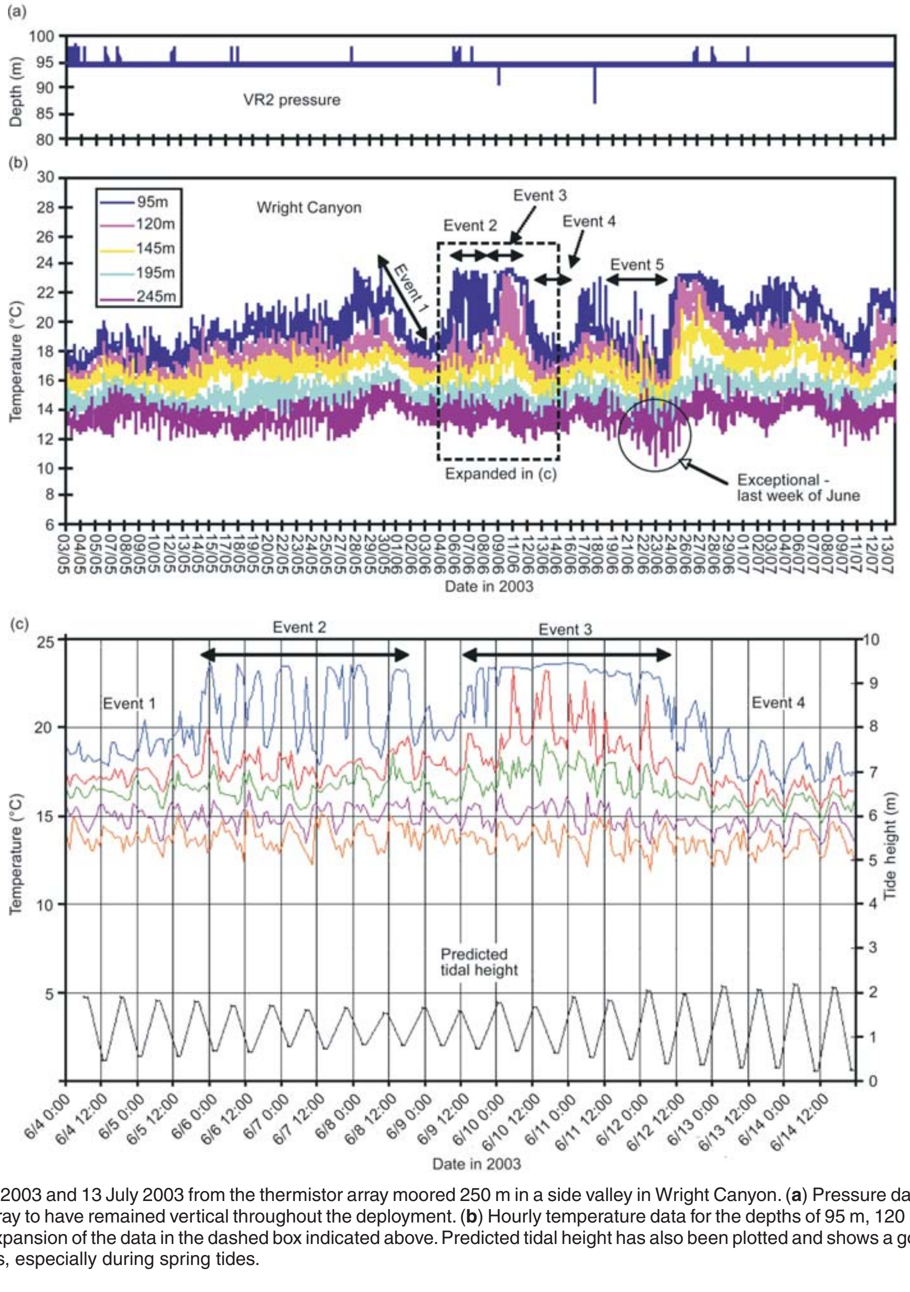

Fig. 8. Data between 3 May 2003 and 13 July 2003 from the thermistor array moored 250 m in a side valley in Wright Canyon. (**a**) Pressure data recorded at the top of the mooring (95 m) show the array to have remained vertical throughout the deployment. (**b**) Hourly temperature data for the depths of 95 m, 120 m, 145 m, 195 m and 245 m (2 m from the bottom). (**c**) Expansion of the data in the dashed box indicated above. Predicted tidal height has also been plotted and shows a good correlation with many of the temperature fluctuations, especially during spring tides.

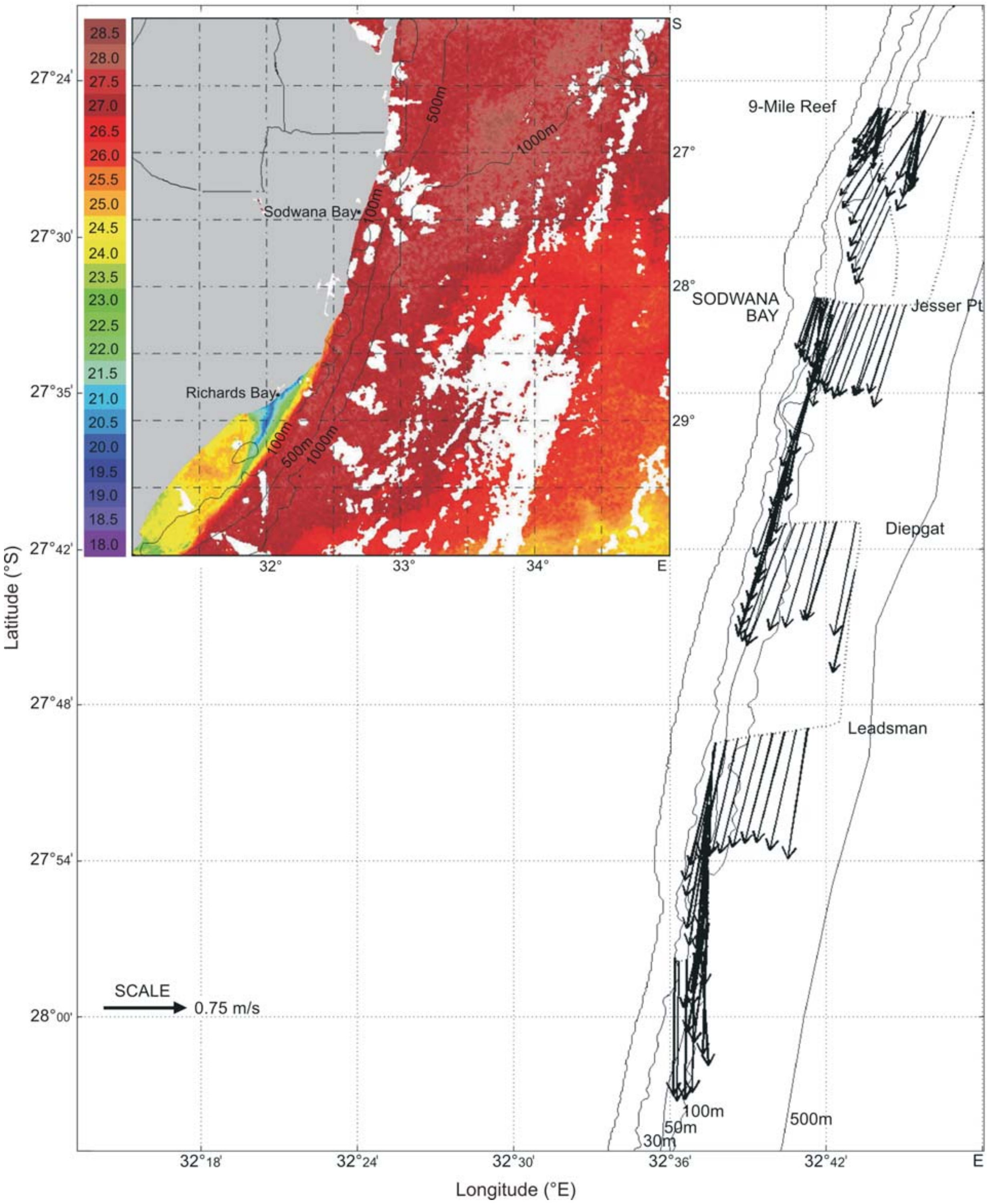

Fig. 9. Velocity data collected on 5 April 2002 using a 150-kHz ship-board ADCP. Stick vectors corresponding to a depth of 12 m indicate a strong southward flow along the shelf edge. SST data in the satellite image (inset) show the Agulhas Current (red) joining the shelf near Sodwana Bay. Scale in °C.

that is, in the coelacanth habitat. It is assumed that because the thermistor array was only 200 m from the side of the canyon, the thermistor data will be representative of temperature against the shelf slope. Below this depth, the range in temperature generally decreased to 2–3°C. The exception was the last week in June, when the range increased to 11–16°C (Fig. 8b).

It is highly probable that the longer-term cooling events, i.e. events 1, 4 and 5, are due to shelf-edge upwelling as a result of the Agulhas Current flowing close to the edge. When this happens, Ekman veering is experienced in the bottom layer, which causes cooler water to move up the slope.[19] Offshore movement of the current a few days later would diminish Ekman veering, resulting in warmer water replacing the cooler water.

The high-frequency fluctuations seen in the temperature records are predominantly linked to tides and the consequent movement of water up and down the continental slope. This is seen in the expanded subset of temperature data in Fig. 8c. The predicted tidal range for the period for the nearest port, Richards Bay, is shown at the bottom of the plot (note that actual tidal height was not available). The maximum tidal range in this area is 1.95 m. The tidal signal is most consistently seen in the deeper temperature data at 195 m and 245 m, in which a good correlation exists (with almost no lag) between a rise in temperature at low tide and a decrease in temperature at high tide. The correlation becomes weak during neap tides when the tidal range is lowest (*c.* 0.8 m). Generally, the tidal signal is also observed in the shallower depth data, but is particularly obvious at 95 m during event 2. Here the large changes in temperature at 95 m are due to the vertical movement of the sharp thermocline at around this depth, i.e. a much greater change in temperature for a given rise and fall of water relative to greater depths where the temperature structure of the water column is less condensed.

In event 3, the situation is almost reversed in that the 95 m data are consistent for 3.5 days at *c.* 23.6°C, while the 120 m data show large temperature fluctuations which strongly correlate with the tidal signal. The only explanation for this is that the sharp thermocline impinging on the shelf slope was deeper on this occasion at around 120 m and that the 95 m UTR was positioned in the warm upper mixed surface layer—a situation similar to that depicted in Fig. 4a, where the thermocline is downward tilting onto the slope.

Thermistor data have shown that temperature in the coelacanth habitat at Sodwana Bay is not as stable as that portrayed by the CTD data and emphasizes the importance of moorings; it is highly variable, ranging between 13 and 24°C with large fluctuations of up to 5°C occurring over only a few hours. However, it may be that coelacanths can avoid this rapid and high variability by moving into deep caves where water exchange will be limited and hence temperatures more stable. This needs to be tested by deploying UTRs outside and inside caves at Sodwana.

The inverse situation, that is, coelacanths in warmer water inside a cave than out, was noted in the Comoros by Fricke *et al.*,[20] with a thermocline appearing within the cave (see their Fig. 10). The fish in the cave were at 22.8°C, when outside it was 18°C. They also suggested that the upper threshold limit for coelacanths is 22–23°C. This suggests that coelacanth distribution might be affected more by the presence of appropriate shelter than temperature.

Oxygen

Figure 2b shows a typical dissolved oxygen (DO) vertical profile found off Sodwana Bay. DO at the surface in all the CTD transects sampled was found to be approximately 3.6 ml l^{-1} with bottom values at a depth of 1000 m of *c.* 3.2 ml l^{-1}. A shallow oxygen minimum (SOM) of *c.* 3.2 ml l^{-1} was observed in all data between the depths of 100 and 250 m. Immediately below this, the DO increased to values similar to the surface, i.e. 3.6 ml l^{-1}, before decreasing to the lower levels at 1000 m. The SOM therefore meets the continental slope at the depths where the Sodwana Bay coelacanths have been found (100–140 m). DO values extracted for 100 m and 140 m in all transects are listed in Table 1 and ranged between 3.0 and 3.2 ml l^{-1}.

The SOM is a characteristic found throughout most of the South-West Indian Ocean. As seen in Fig. 7 it overlaps the 15–19°C layer mentioned above and hence follows a similar trend, being deeper in the equatorial regions and shallower in the south adjacent to the African continent. Near the Comoros these data (collected in August 2003) show SOM values of 2.9 ml l^{-1} in the depth range of 200–325 m in which coelacanths are found. The Sodwana Bay SOM levels reported here are of a similar level to those at the Comoros in Fig. 7. Interestingly, Hissmann *et al.*[4] measured DO values of 3.5 ml l^{-1} at cave entrances in the Comoros, indicating some variability in the coelacanth habitat there.

The significance of varying levels of DO on the physiology of the coelacanth is not yet understood. Work by Hughes and Itazawa[18] suggests that the optimum temperature for the uptake of oxygen in coelacanth haemoglobin is 15°C. This implies that the Sodwana coelacanths should rather be living at greater depths of around 200 m instead of 100–140 m. However, observations from submersible indicated there are fewer caves deeper than 140 m (that is, below the Pleistocene terraces[3]) and so it is possible, given their apparent affinity to caves, that these coelacanths could become stressed when water temperature increases substantially above the optimal oxygen uptake temperature of 15°C.

Currents

An ADCP survey was undertaken along the shelf edge between 9-Mile Reef and Leven Canyon on 5 April 2002. The horizontal velocity data are shown in Fig. 9 for the 12 m depth layer (i.e. 1st bin). Note that despite the vessel being restricted to a minimum depth of 30 m, it was still possible to survey the outer region of this shallow shelf.

The data showed a strong southward flow throughout the survey area, with some attenuation in velocity as would be expected on the shelf with the close proximity of the Agulhas Current. As reported above, measured velocities on the shelf near 9-Mile Reef commonly reach 0.5–0.75 m s^{-1} but rarely exceed this maximum (M. Roberts, unpubl. data). The highest surface velocity in this survey was 120 cm s^{-1} observed offshore in the northern 9-Mile transect and in the south just north of Leadsman Canyon (120 cm s^{-1}). The offshore maxima between these transects were 80 and 100 cm s^{-1}. The mean surface velocity offshore of the shelf edge was *c.* 80 cm s^{-1}. To determine whether these velocity values are common when the Agulhas Current flows close to the shelf edge will require the use of current meter moorings in future studies.

Vertical velocity sections to a depth of 150 m along these transects normal to the shore indicated that velocity not only decreased quite rapidly with depth for all transects, but also that velocities in the water column were lowest in the north (Fig. 10). The horizontal velocity gradient along these transects was more complex than anticipated; a steady offshore gradient of increased velocity at any given depth was expected, and not the zones of lower velocity such as seen in the southern Diepgat Canyon transect.

The satellite SST image shown in Fig. 9 offers an explanation for these unexpected observations: the Agulhas Current proper joins the Maputaland shelf only in the vicinity of Sodwana Bay and appears to have an undulating inshore boundary particularly along the shelf edge. This undulating boundary accounts for both the weaker current velocities measured inside of the 120 cm s^{-1} velocity maximum at 9-Mile Reef and for the complex vertical velocity structure observed along the slope, which ranged between 20 and 80 cm s^{-1} in the depth zone of 100–140 m.

It was not possible to measure velocities accurately using a shipborne ADCP in the canyons due to their narrowness. Nonetheless, very slow and sometimes no currents were detected on *Jago* dives in those canyons where coelacanths were recorded. Also, Trimix divers in Jesser and Wright canyons reported the relative absence of currents just above the substratum. Of course, these anecdotal reports need to be confirmed by a series of velocity measurements using current meters deployed in the coelacanth habitat both inside canyons and on the exposed shelves between canyons.

By comparison, velocities measured in the coelacanth habitat by Hissman *et al.*[4] on the steep slopes of the Comoros Islands were much less than those found off Sodwana Bay, that is, 4.9 cm s^{-1} at 159 m, 3.6 cm s^{-1} at 255 m and 3.1 cm s^{-1} at 273 m. Under these conditions, *Jago* observed coelacanths to move away from their caves at night and to swim slowly along the slopes for distances of up to 10 km. The low-velocity environment no doubt ensured the return of these animals to their caves

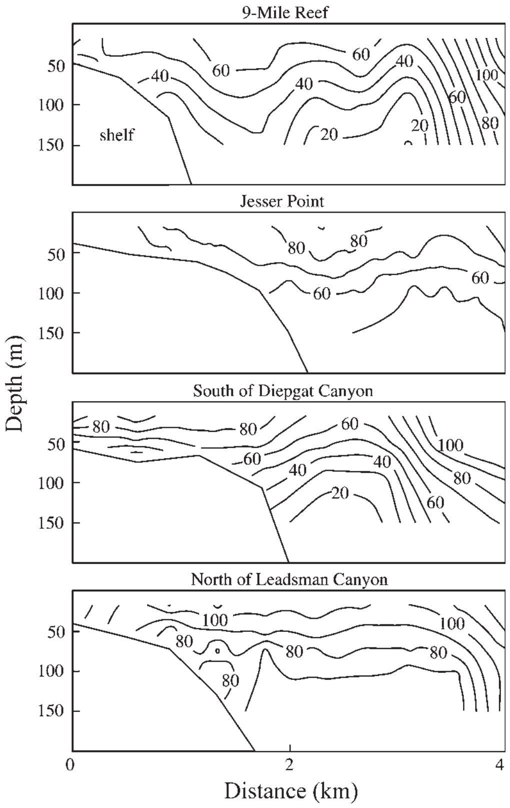

Fig. 10. Vertical velocity sections along shore-normal transects shown in Fig. 9. Contour intervals are 10 cm s^{-1}.

with ease.[4] The low current velocity in canyons, and immediately above the substratum between canyons, enabled coelacanths to migrate within individual canyons and between Wright and Jesser canyons.[2]

One individual (No. 14) moved from Jesser to Wright Canyon, a distance of 4 km, and was then observed again in Jesser three days later,[2] clearly exhibiting mobility along the shelf slope.

Presumably, to move northeastwards (upstream) they would either have to wait for periods of weak current, or use the boundary layer of lower velocity which exists at the water–slope interface.

To understand which of these is applicable requires detailed experiments using deployed current meters and electronic tag telemetry.

Conclusions

1. The seventeen CTD sections collected during four cruises in 2002 and 2003 indicate the temperature range in the Sodwana Bay coelacanth habitat between the depths of 100 and 140 m to be similar to that found in the Comoros Islands, i.e. 15–22°C cf. 15–19°C in the Comoros. This is because these isotherms relative to the Comoros become shallower southwards along the African coast. Because caves and overhangs are also more abundant in the 100–140-m depth range near Sodwana Bay, it is not possible to determine yet which of these two parameters is the most important in determining coelacanth habitat.
2. A 2.5-month-long time series of hourly data collected by a thermistor array deployed near a known coelacanth cave in Wright Canyon indicates this environment to be much more variable than implied by the CTD data, with temperature changes of 16–24°C occurring in a day. This variability is largely caused by the diurnal tide and is greatest during spring tides.
3. The finding of a coelacanth on the shelf edge at a depth of 54 m was coincident with one of the most significant upwelling events between 1994 and 2005, when temperatures at this depth decreased to 17–19°C.
4. Dissolved oxygen levels in this depth zone were found to range between 3.0 ml l^{-1} and 4.8 ml l^{-1} compared to 3.5 ml l^{-1} in the Comoros. The low oxygen values near Sodwana Bay are a result of the SOM, which becomes shallower, as do the temperature isotherms in the southwest Indian Ocean compared to the tropical latitudes and particularly in the Agulhas Current.
5. Current velocities measured using a ship-board ADCP in the depth range 100–140 m at Sodwana were considerably higher than those measured in the Comoros habitat using a current meter (20–60 cm s^{-1} cf. 3–4 cm s^{-1}) and may be an important factor explaining the coelacanth's occupation of the canyons found along the Maputaland shelf-break. However, coelacanths can swim from Jesser to Wright canyon, suggesting that those at Sodwana are not always restricted to the shelter of the canyons by the powerful Agulhas Current.

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