African Coelacanth Ecosystem Programme: An overview of the conference contributions

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***Latimeria chalumnae* is the icon for the multidisciplinary, multinational African Coelacanth Ecosystem Programme (ACEP) dedicated to improving the understanding of biological and other processes that support marine life. This article provides an overview of contributions made at a conference hosted by ACEP at the end of 2003. It also reviews significant developments regarding coelacanth conservation which have taken place since the conference. Delegates at the meeting concluded that the integrated regional, ecosystem approach that had been adopted by ACEP should continue. Underwater observation and exploration, however, should be supplemented by more experimental and technical analyses in order to answer long-standing questions related to coelacanths and other organisms.**

Introduction

Coelacanths became known as a distinct taxonomic group when Louis Agassiz published his book *Recherches sur les Poissons Fossiles* (1844).[1] Since then, many fossil coelacanths have been discovered,[2] but none of the fossils appears to be more recent than about 60 million years (Myr) ago, suggesting that the group became extinct 60–70 Myr ago. Then in 1938 a living coelacanth (*Latimeria chalumnae*) was discovered by Marjorie Courtenay-Latimer among specimens on a trawler which had been fishing off East London, South Africa. This fish was described by J.L.B. Smith[3–7] in an atmosphere of scientific excitement, scepticism and doubt.[8] The media considered this to be the zoological discovery of the century. This was the first of three singular discoveries which shaped South African coelacanth research.

The second discovery, by Captain Hunt in 1952, resulted in the flight of the Dakota 6832 from South Africa to the Comoros Islands to retrieve the specimen. Smith was so concerned that the specimen would be lost to science that he persuaded the prime minister, D.F. Malan, to provide a South African Air Force plane for this purpose.[8,9] This discovery led to a number of publications on the morphology of coelacanths.[9–13] It also opened the door to other researchers in the Comoros, primarily from France.[14–16] Initially, Smith considered the second specimen to be a new genus and species, and named it *Malania anjouanae*,[9] but later it was realized that the anatomical differences were due to injuries sustained during capture and preservation of the fish. It was indeed *Latimeria chalumnae.*

The third discovery was remarkable in that intrepid divers[17] found and photographed coelacanths in a canyon in the Greater St Lucia Wetland Park (GSLWP), KwaZulu-Natal, South Africa, on 27 November 2000. This discovery was not entirely accidental. On the basis of their understanding of coelacanth habitat, these divers predicted that coelacanths might be found in the canyons of the GSLWP and mounted an earlier expedition in 1998. On that occasion they did not find coelacanths, but they collected biological samples and obtained video footage of the canyon habitat down to depths of 140 m.[18] The 2000 discovery of a colony of coelacanths in a marine protected area (MPA), led to immediate protection of the coelacanths and their habitat by the Minister of Environmental Affairs and Tourism, Valli Moosa. Shortly thereafter, a management and conservation strategy was drawn up by Ezemvelo KwaZulu-Natal Wildlife and the Department of Environmental Affairs and Tourism.[19] The plan called for a research project to better understand the coelacanth, its relation to the habitat and its conservation status. It also recommended the fostering of environmental education and public awareness. The existence of coelacanths in an MPA, which is in addition a World Heritage Site, placed an added, urgent responsibility upon South Africa to develop a well-informed management and conservation strategy. Policies and activities developed for the GSLWP could serve as a model for development of protected areas for conservation of coelacanths and their ecosystems in the Comoros as well as Tanzania and Madagascar. Such new protected areas are becoming priorities as the number of coelacanths caught is increasing annually.[20]

In response to the urgency to act, an inclusive planning workshop was sponsored by the National Research Foundation in September 2001. Ninety participants were responsible for the multidisciplinary South African Coelacanth Conservation and Genome Resource Project. An ecosystem approach was adopted because coelacanth relationships with and responses to the physical and biological environment need to be defined in order to answer questions regarding coelacanth ecological, evolutionary, life-history and behavioural adaptations. Similarly, a sound understanding of the relationship between coelacanths and their physical, chemical and biological environment is a prerequisite to an informed management and conservation strategy.

The project was launched in April 2002 by Dr Ben Ngubane, Minister of Arts, Culture, Science and Technology. He called for the project to embrace the New Partnership for Africa's Development (NEPAD) and to work with partners in the Comoros, Kenya, Madagascar, Mauritius, Mozambique, Seychelles and Tanzania. The transfrontier growth of the programme into a multinational initiative resulted in a name change to the African Coelacanth Ecosystem Programme (ACEP). The name incorporates the iconic coelacanth of Africa with the 'coelacanth ecosystem', which covers the geographical range of the partner countries and operates in depths from 40 m to about 1000 m.

ACEP's catchphrase, 'Window to the Past, Door to the Future', refers to opportunities that coelacanths have provided which enable African scientists to ask whether the coelacanth genome is truly ancient, to study geological history and examine evolution of the biological communities in which coelacanths live. The 'door to the future' depicts the opportunity to build capacity, promote understanding, influence management and conservation strategies, build partnerships and address issues of socio-economic development and achievement of Millennium Development Goals.

The conference of November 2003 enabled ACEP to place its findings before the national and international community, in order to assess whether its goals, vision and procedures were correct. A workshop following the presentations reviewed ACEP and its multidisciplinary approach. Papers from researchers elsewhere in the world were presented to

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broaden experience, exchange ideas and promote overall understanding of coelacanths and their ecosystems.

Exploration and conservation of the oceans

The discovery of coelacanths in the relatively shallow heads of canyons within the popular GSLWP, which is frequented by scuba divers, strongly reiterated the need to explore the deeper waters of the Western Indian Ocean. Clearly, if these large, sedentary fish have remained undetected for years, what else of great potential interest to humans awaits discovery in our oceans? In her keynote address,[21] Sylvia Earle provided a broader perspective of the need to explore, understand and conserve marine ecosystems. She pointed out that 97% of the biosphere is ocean, and that it is home for the greatest biodiversity, with nearly all the major divisions of life occurring there. Yet, just as the discovery of coelacanths in the GSLWP demonstrated, the oceans are virtually unexplored. Only a small fraction of 1% of the ocean is protected.[21] Clearly, far greater investment in marine protected areas is required. Arguing generally for an improved understanding and greater protection of the oceans, Earle indicated the huge impact that seas have on climate, weather, temperature, planetary chemistry and every aspect of life on land, even in places distant from the seas. Every breath one takes and every drop of water one drinks has its origin in the ocean.

She sees the coelacanth as a symbol of hope that everyone should use to energize themselves in order to make a difference, arguing that:

> 'What we do — or fail to do — in this first decade of the new millennium will likely shape the course of the next thousand years.' (ref. 21, p. 418). What we do should be as '…enduring as that of the great fish that draws us together today.'

The coelacanth is rapidly becoming an icon for marine research, education and socio-economic development of people who depend on the sea throughout the Western Indian Ocean.

A regional approach

Conservation status of any population within the species distribution range can be assessed only once the behavioural, ecological and physiological adaptations are compared throughout the range. From the outset a regional comparative approach was adopted in which Comoros, Kenya, Madagascar, Mozambique and Tanzania became important partners on the project. This partnership was strengthened by a regional decision to use the coelacanth as an icon for a broader biophysical study of the ecosystem of the Western Indian Ocean, with high priorities being placed on capacity building and conservation.

As the project progressed, partnerships with Mauritius and the Seychelles were established. ACEP is now a NEPAD flagship project of the Coastal and Marine (CosMar) sector. At the conference, leaders of the various national delegations gave presentations on the manner in which each country might contribute to and benefit from transfrontier collaboration.

For several years the Comoros have been considered to be the natural home of coelacanths.[22,23] An expectation, therefore, was that coelacanths would be most closely adapted to the Comoran volcanic lava habitats. If this is correct, then the South African population, at the southerly extreme of the known distribution range, may be in an atypical, marginal, habitat. The GSLWP population might be ephemeral.

Multidisciplinarity

To determine the conservation status of a species it is necessary to define its range of habitat tolerance and sensitivity to change. Studies in the Comoros suggest that coelacanths have a narrow range of habitat tolerance, being restricted to hard surfaces and caves within lava, are sensitive to temperatures above 21°C, avoid strong currents, require water with a high oxygen concentration and have eyes that are sensitive to strong light intensity. There is a general expectation that species with a narrow habitat tolerance (stenotopes) are short-lived. Small changes in environmental conditions might impose strong selection pressures on such species. These pressures would lead to evolutionary adaptations or cause extinction. In contrast, species which have a broad habitat tolerance (eurytopes) are likely to be long-lived.[24,25] The fact that *Latimeria* seems to have stenotopic characteristics but is long-lived is an apparent anomaly that requires a multidisciplinary study of its adaptations to the environment.

Scientific research will ultimately place the coelacanth correctly on the stenotopic–eurytopic continuum, and therefore define its conservation status. Conservation, however, involves more than science. It includes management of human activities and the willing, active participation of informed communities. Public understanding, environmental education and community participation become crucial ancillaries to science within conservation programmes. ACEP adopted a multidisciplinary approach from its inception that embraces science, the humanities, education and training. It also involves promotion of environmental education and public awareness.

Physical and biological sciences

Geosciences

The submarine canyons of the northern KwaZulu-Natal continental shelf were the initial focus of attention because they appeared to be sheltering coelacanths. A multibeam, bathymetric survey of 23 submarine canyons was undertaken.[26] The bathymetric maps contributed to a definition of the physical, structural habitat of coelacanths and were used to guide the manned submersible, *Jago,* to caves and broken habitats which provide coelacanths with shelter. The bathymetric data and maps were developed further to provide the basal layer of a marine Geographical Information System (GIS) around which to build all georeferenced physical and biological data of ACEP.[27]

The colour-draped maps[26] and geological data derived from the bathymetry were cost effective in terms of directing *Jago* searches, so that ship, submersible and research time were not wasted. The study provided a general description of the submarine canyons and discussed their possible origins. It gave some detail on canyon and shelf morphology.[26] Direct observation and collection of material from the *Jago* were used to verify composition of the substratum.[17,18,23] The bathymetry and GIS data facilitated studies of habitat use and accurate plotting of coelacanth movement between caves and canyons.[23] Many caves seemed suitable for use by coelacanths, but were not occupied at the time that they were visited by the *Jago.*

In contrast to those who believe that the Comoros are the home of *Latimeria chalumnae,* the geologists consider that the numerous canyons along the northern coast of Mozambique are more likely to be the continental home of coelacanths and the origin of all other populations.[26] The geomorphological evidence suggests that Port St Johns may be the southernmost limit to coelacanth distribution.

Oceanography

Ocean currents, temperature, oxygen, and light intensity all seem to affect the distribution and activities of coelacanths in the Comoros[23,28–31] and to define their habitat range.[32]

Oxygen and energy conservation

In a morphological study of the gills of *Latimeria chalumnae* from the Comoros, it was found that coelacanths have a much smaller gill surface-area to body volume ratio (*c.* 18 mm^2/g body mass) than most other fishes.[33] The total length of their gill filaments was small, and the tissue barrier between dissolved oxygen in the water and the blood was thicker than for most other fishes — combined factors which result in a poor diffusing capacity. *Latimeria* appears to be morphologically ill-equipped to take up oxygen readily. Similarly, knowledge available regarding blood physiology confirms poor oxygen uptake ability.[32,34,35] Hughes[33] concluded that, 'a very sluggish mode of life is indicated and excessive exercise would result in hypoxic stress'. Behavioural studies[36] of coelacanths suggest that coelacanths conserve energy, require oxygen-rich waters and are probably not capable of swimming strongly for protracted periods.

In contrast to most fishes in which there is a significant increase in the number and relative size of gill filaments as the fishes grow, in *Latimeria chalumnae* there is virtually no change in number or the proportional size. This suggests that as coelacanths grow they become less well equipped to take up oxygen. Intuitively, there is an expectation that adult coelacanths should live in water which is calm to minimize energy used to counteract currents, where dissolved oxygen concentration is high, and where temperatures favour oxygen uptake by the blood but are cool enough to keep metabolic rates low.

Currents

When ACEP was established, two intriguing questions concerning currents required answers. First, given the indications that coelacanths are 'sluggish' and keep their metabolism low to avoid hypoxic stress,[33,34,36,37] how do they cope in the strong Agulhas Current that rushes though the Greater St Lucia Wetland Park? It was assumed that as an energy-saving ploy, *Latimeria* should seek shelter from strong currents.

This question may have been answered. Study of current profiles over the canyons has shown that while currents are strong in surface waters, they diminish with depth and are virtually non-existent in the canyons.[23,38] Similarly, just above the substrata of the areas between canyons, there is a boundary layer of approximately 10 m depth in which currents were so reduced at the time of the study that coelacanths could swim between canyons. In essence, currents were absent from the demersal habitat occupied by *Latimeria* in South Africa during the study period. The lack of currents in GSLWP canyons makes them suitable for coelacanths.

The second question relates to the geographic origin of the South African population. J.L.B. Smith[8] and others who followed him[22] believed that the 1938 *Latimeria chalumnae,* the holotype, was carried to East London by currents from regions to the north of South Africa. The discovery of almost 200 coelacanths in the Comoros between 1952 and the present gave rise to the notion that the Comoros are the ancestral home of the African coelacanth, from which populations in Madagascar, Kenya, Tanzania, Mozambique and South Africa were carried by strong currents.[22,23] It was speculated that the very small populations in each country are in effect ephemeral founder populations. For this hypothesis to have credence, it is necessary to establish that the currents do indeed follow a course that could carry coelacanths from the Comoros to South Africa, perhaps via Mozambique as suggested.[22]

Oceanographic data[38] show that the eddies in the Mozambique Channel are such that if coelacanths originated in the Comoros, their journey to South Africa would be long and complicated. They would probably be carried out into the channel by the eddies, perhaps reaching Madagascar, or brought back inshore to Mozambique.

Whether coelacanths would allow themselves to be swept from their home ranges will only be answered by further research. When travelling at two knots in pursuit of a coelacanth, *Jago* was unable to keep up; the coelacanth pulled ahead and was lost from view. Coelacanths are not helpless swimmers. They also have strong homing capabilities[39] suggesting that, if they were being carried away from their home range, they would be aware of this and return to sheltered areas. It is possible that coelacanths could be transported away from their homes in strong currents and lose the energy to battle against the currents, but this seems unlikely in normal conditions.

Temperature and depth

Physiological evidence related to respiration and oxygen affinity of haemoglobin,[32] plus records of coelacanth distribution with respect to environmental temperature profiles suggest that the normal temperature range for coelacanths is 16–20°C in the Comoros,[30,37] South Africa[23] and Indonesia.[40] Until 1998, the highest temperature recorded for coelacanths was 22.8°C[29] in a cave at the Comoros, but a temperature above 24°C[37] was then observed. This highest temperature was previously considered to be beyond the upper end of the normal tolerance range,[37] especially as *Latimeria* is likely to be in respiratory distress in temperatures above 20°C.[37] Warmer water increases metabolic rate and therefore oxygen demand. The reduced oxygen content of warm water further exacerbates respiratory and metabolic stress. Coelacanths in caves where the temperature is above 20°C would need to remain quiescent to keep the metabolic rate, and oxygen demand, as low as possible.

Latimeria is subject to both seasonal and daily changes in temperature. In the Comoros, most specimens were found between 16.5–18°C in May and 18.5–20°C in November.[29] Coelacanths in caves also seem to be relatively tolerant of daily fluctuations in temperature. In a 22-hour period a temperature fluctuation of between 18.7–22.3°C was recorded in association with tides: higher temperatures were recorded during high tides at the Comoros.[29] Similarly, South African coelacanths can tolerate a temperature range of 6°C within a single day.[38] The lower temperature limit for *Latimeria* is not known.

Oceanographic data[38] collected in the Greater St Lucia Wetland Park show that the 22°C temperature isotherm hovers around 100 m, which is about 100 m shallower than in the Comoros. If coelacanths are as sensitive to temperature as is suggested by the available evidence, then the South African coelacanths, in the heads of the canyons, are living for much of their lives at the ceiling of their temperature tolerance range. Confident conclusions regarding temperature tolerance and impacts of temperature on behaviour cannot be drawn until a more rigorous study has been undertaken using physiological probes and biotelemetry.

Water quality: oxygen, salinity and light extinction

Oceanographers measure a variety of parameters associated with water quality, of which the most relevant to coelacanths are likely to be dissolved oxygen concentration, salinity and light intensity. As indicated above, their gill morphology and blood physiology suggest that coelacanths should remain in oxygen-rich water. This is not the case, however, because data show that the depths at which they live throughout their known range in the Western Indian Ocean are within the areas of oxygen minima (see Fig. 7 of ref. 38). It seems that coelacanths will occupy caves in which temperature and oxygen conditions are less than optimal. This suggests that the benefit derived from the occupancy of caves takes precedence over the requirement for oxygen-rich, cool waters. Of course, if oxygen concentrations were to drop to levels that were life threatening, then coelacanths would be forced to abandon their caves in search of oxygen-rich zones.

A profile of the salinity range around the Western Indian Ocean (see Fig. 7 of ref. 38) indicates that coelacanths are living in water of slightly higher salinity than at depths above and below them. At present, there are no data to show the effect of salinity on coelacanths so this factor requires further investigation.

Caring researchers are reluctant to disturb this ancient creature in its natural habitat. There is an assumption that *Latimeria* eyes are unable to cope with bright light, so scientists avoid shining lights on to the eyes of what might be dark-adapted animals. A culture is developing which encourages those using manned submersibles and remotely operated vehicles (ROVs) to exercise care and use infrared illumination where possible. When white lights are used, the brightness is increased gradually over time to allow the coelacanths' eyes to adapt. Although the scientific evidence of light sensitivity is not irrefutable, it is sensible to adopt the precautionary principle. The transparency of the water and relatively shallow depths at which coelacanths live in Sodwana Bay means that they are exposed to higher light intensities than in the Comoros. Despite this, some were found in full light at the mouths of caves during the day and even between caves. If *Latimeria* were truly sensitive to light, then it might be expected that they would remain deep in the caves throughout daylight hours.

In their review, Modisakeng *et al.*[40] report that Comoran and Indonesian coelacanths receive a narrow band of light (approximately 480 nm) and that both have identical RH1 and RH2 pigments with optimum light sensitivities (λ_{max}) of 485 and 479 nm, respectively, showing detection of a narrow colour range. They discuss the genetics which underlie loss of pigments under low light conditions. The discovery of coelacanths in relatively shallow water and good light conditions off Sodwana (from 54–140 m depth) calls for a further evaluation of coelacanth vision and light sensitivity.

Oceanographic findings show that the South African coelacanth population is living close to the upper limit of its temperature tolerance range, in an oxygen concentration that appears to be sub-optimal, at a slightly higher salinity than surrounding water and that, by virtue of its demersal habits, it is not normally subject to strong currents.

Biology

A first step in exploring adaptations of coelacanths to their biological environment is to determine species composition of the habitats and assess interspecific relationships. If *Latimeria* were tightly adapted to its biological environment through obligate interspecific relationships, then it would be reasonable to expect it to be a member of a community of ancient creatures. This is not the case. *Latimeria* is a living fossil co-existing with younger species.

An alternative which might reflect narrow adaptation is that the species composition would be much the same throughout the geographic range of coelacanths. An initial comparison[42,43] of the fish communities of the Comoros and Sodwana shows that the Sodwana Bay coelacanth habitat is richer in species (140 taxa) than the Comoros (88 taxa). Only 32 taxa occur in coelacanth habitats in both the Comoros and Sodwana Bay, but the authors[42,43] are convinced that these early comparisons seriously underestimate the number of species in both study areas. Further research may show that the total number of species in each habitat is greater than present knowledge indicates. The proportion of species common to both areas might also be modified, but such research is unlikely to change the conclusion that the adaptation of *Latimeria* to its co-inhabitants is rather loose, with perhaps no obligate associations except perhaps for parasites.

The fishes that occur in the canyons may interact directly with *Latimeria* as prey, predator or competitor (for food), or, for a few species, they may have no direct interaction at all. Insightful first endeavours to define relationships between coelacanths and other fishes have been provided.[18,42,43]

Five habitat types, each supporting distinct biological communities[18] were recognized in a study of species–habitat relationships of canyon ecosystems. This study focused on invertebrates, but included some fish.[18] Overall, the canyons and deep reef ecosystems were found to be rich in species, with the canyon margins being the richest. It was clear to the researchers[18] that a great deal of work needs to be done on deep reefs, not only of South Africa, but world wide, as these are rich, near-shore environments that have been strangely overlooked. As Sylvia Earle[21] pointed out, the undersea environment is unexplored, even that which is on our doorstep.

Biological surveys throughout the Western Indian Ocean are consistently demonstrating the great richness of species and exposing our ignorance and the need for further research. Much needs to be explored and understood if humans are to benefit through wise management of the resource. The relationship of coelacanths to the rich invertebrate communities with which they live is virtually unknown except that invertebrates have occasionally been found in the stomachs of *Latimeria.*

Coelacanth studies

Distribution

As a result of scuba,[17] manned submersible,[23] and latterly ROV[44] studies, 26 individual *Latimeria chalumnae* can be identified in the GSLWP. Each individual has a unique set of white markings that facilitates identification. During the existence of ACEP, 29 coelacanths have been caught in Tanzania, with information regarding 21 reported in this issue.[20] In the Comoros, two additional coelacanths have been caught, including one from Moheli Island, from which coelacanths had never been recorded previously. Three more coelacanths have been caught in Madagascar, including one north of Tulear in a canyon near to Nosy Lava. The spate of catches in Tanzania and Madagascar may be attributed to increased fishing effort in deeper water using gill nets. Greater awareness of the significance of coelacanths has also led to catches being reported by fishermen. There are suggestions that activities of offshore trawlers might have driven coelacanths inshore where they get caught.[20] The African coelacanth, *Latimeria chalumnae,* is now known from South Africa, Mozambique, Tanzania, Kenya on the east coast of Africa, and the island states of the Comoros and Madagascar.

Greater St Lucia Wetland Park

The objectives of the study in the Greater St Lucia Wetland Park were to determine the population size of coelacanths, study their behaviour, movement and use of habitat, and to establish their conservation status. An important goal is continually to improve understanding in order to provide recommendations for conservation and management to augment those prepared initially.[19]

Despite the fact that the canyon habitats of South Africa differ considerably from those of the volcanic Comoros, some aspects are similar. In both localities, coelacanths occupy caves or sheltered habitats during the day and most are found within the 16–22.5°C isotherms, which are approximately 100 m deeper in the Comoros than in South Africa. Coelacanths may be found singly or in groups in the caves; they show site fidelity, but may use several different caves within the home range. In the Comoros, a home range might extend for about eight kilometres.[39] In South Africa, the sizes of home ranges have not been defined, but individual coelacanths are known to move between Jesser and Wright canyons, approximately four kilometres apart.[23]

As yet the population size of *Latimeria* within the canyons is unknown. A great deal more work is required. Even though new individuals were found on every *Jago* and ROV expedition, the population is assumed to be relatively small. The three canyons in which coelacanths have been found are separated by more than 50 km. In the Comoros, it appeared that most caves that could be occupied by coelacanths were used and that some were saturated.[28,29] By contrast, many caves in the canyons off South Africa which appear to be suitable were unoccupied when visited by the *Jago* and the ROV. Coelacanth carrying capacity in the canyons is unknown, but the poor occupancy of caves relative to the Comoros suggests that the canyons could accommodate a larger population. If, however, conditions in the canyons are sub-optimal for coelacanths, then the carrying capacity is likely to remain low.

A potentially valuable observation when determining occupancy of caves is that when coelacanths are at rest in caves, they remain stationary, just above the substratum. This resting position is maintained by slow fin movements, which scour and heap the sand into characteristic tell-tale patterns which can be used to determine whether caves, which are empty when visited by researchers, had accommodated coelacanths in the recent past.[45]

In every area in which coelacanths have been studied, several of the fundamental questions, some dating back to when they were posed at the time Marjorie Courtenay-Latimer first discovered a living coelacanth, remain unanswered or only partially answered. It is not known where and when coelacanths breed, how they copulate, whether courtship is elaborate or simple, whether they practise parental care, where the young reside or the period of gestation. Questions regarding population structure, life history, longevity, migration patterns, site fidelity, feeding, physiology, social interactions and hierarchies, family structure and kin-related behaviour, and many more are all awaiting comprehensive answers from detailed studies. The opportunities to conduct in-depth investigations are now available.

Molecular studies

Two overriding interests intrigue scientists, and indeed the human audience as a whole: one, whether land vertebrates, and hence man, did indeed arise from a coelacanth ancestor or some other fish; the other fascination is the manner in which the huge transition of vertebrate life from water to land took place about 360 Myr ago. J.L.B. Smith's book, *Old Fourlegs,* enables one to envisage the four lobed fins of coelacanths pulling them out of water onto land, where they gasped for breath under the selective pressures that might lead to the evolutionary adaptations that would enable them to become amphibians. Those of us working on coelacanths would like to imagine that they were the tetrapod ancestors, but current molecular studies of phylogeny suggest that, of the lobe-finned fishes, the lungfish are the more likely candidates.[41,46–53] The data, however, are not conclusive.[48] Even a diphyletic origin of tetrapods has been considered.[48] Naturally, none of the extant species of lungfish or coelacanth has claims to providing the tetrapod ancestors. If the tetrapod ancestor was a coelacanth, it would probably have been a freshwater or estuarine form, and not the deep-sea dwelling *Latimeria.* Nevertheless, extant lungfish and coelacanths do provide access to what might be ancient genomes of great evolutionary interest.

As part of the ACEP initiative, Modisakeng *et al.*[41] reviewed the current status of molecular research published for both the African (*Latimeria chalumnae*) and the Indonesian (*Latimeria menadoensis*) coelacanth. They pointed out that in addition to studies related to tetrapod ancestry and phylogeny, access to coelacanth tissue from Africa and Indonesia has led to several major contributions. Comparison of the recently completed *L. menadoensis* mitochondrial sequence with that of *L. chalumnae* revealed a 4.28% difference between the two species and provided an estimate of the divergence time between the two species at 40–30 Myr ago. A number of large gene families such as the *HOX*, *protocadherin* and *heat shock protein* clusters have been characterized. Furthermore, the recent successful construction of a large-insert (150–200 kilobase) genomic library of the Indonesian coelacanth will prove to be an invaluable tool in both comparative and functional genomics.

Population genetic studies have shown that the African coelacanths throughout their distribution range are very similar and might be considered to be a single gene pool.[22] This finding has been used as evidence to support the contention that populations found in locations other than the Comoros were washed there from those islands. The South African population might be a founder population that arose from a single pregnant female, washed to the Greater St Lucia Wetland Park, where it gave birth to its young. Genetic fingerprinting could test this hypothesis, unravel kin relationships and determine the conservation status of the population. An inbred population would be vulnerable to extinction, but one with broad genetic variability would be more robust. A non-destructive, safe method of scale collection developed by the *Jago* team[54] may be used for such an evaluation.

A relatively homogeneous gene pool can also be explained by gene flow which takes place between the geographic localities through active movement of coelacanths.

Data management and GIS

ACEP has developed a Geographic Information System to integrate, analyse and map all spatial data generated within the programme.[27] Disciplines combined within the GIS are marine biology studies, oceanographic surveys and geophysical exploration as well as the observations made and footage taken from research submersibles. The core data in the GIS are based on deep marine ecosystems and the coelacanth. The geographical coverage includes all participating countries from which existing data, as well as newly generated data, are included. Over and above the utility of the GIS as a tool for science, the GIS has been used for interactive environmental education purposes, and to generate public awareness.

Conservation, public awareness and environmental education

In his keynote address at the conference, Erdmann[55] demonstrated how the Indonesian authorities had acted with great responsibility and foresight to conserve coelacanths, and used the discovery for environmental education purposes as a flagship species and as a source of pride in the Bunaken National Marine Park. The exercise has significantly raised local and national interest in marine science, and awareness of marine conservation issues in general. Similarly, ACEP is using *Latimeria chalumnae* as a regional icon for marine research, having mounted region-wide environmental education programmes, which were discussed in sessions at the conference. Erdmann[55] correctly points out that the experiences gained and lessons learned in the conservation campaign for the Indonesian coelacanth are likely to be of interest to other nations in the Western Indian Ocean, which are using the coelacanth as a symbol to promote research into the marine environment, to raise popular awareness and to develop a regional system of best practice. There is also a drive to develop new MPAs, which would include conservation of coelacanths. The greatest urgency for a protected area is in Tanzania, where an unprecedented number of coelacanths were caught in three years.[20]

Discussion

Reviewing the past, plotting the future

A workshop to review ACEP on the last day of the conference concluded that the multidisciplinary, ecosystem approach which had been adopted should continue to be pursued. It was acknowledged that ACEP was fulfilling a much-needed role along the east coast and within the Western Indian Ocean, as its broad-based, biophysical approach served far more than simply coelacanth studies. A better understanding of the processes that support biodiversity and fisheries is emerging. Such knowledge can ultimately benefit millions of people of the region who are dependent upon marine resources.

Regarding coelacanths, many questions have remained unanswered since they were first posed by J.L.B. Smith and Marjorie Courtenay-Latimer in the late 1930s. Even the very substantial contributions by Fricke and his team over a number of years of research in the Comoros and Indonesia[28–31,39,40] have not yet answered fundamental questions related to life-history, ecology, physiology, behaviour, demographics and interactions with both the physical and biological environments in which coelacanths live. In future, exploration and observational research, conducted by manned submersibles and ROVs, will continue to play a major role in coelacanth studies, but the level of technical and experimental research must be elevated so that long-term data are collected through biotelemetry, underwater recording systems and physiological probes in order to answer elusive questions. A new era of undersea research off Africa needs to be launched which will be more technically sophisticated and efficient.

Evolution

Interest around the world regarding the apparent evolutionary stasis of this 'living fossil' remains intense. How could this fish have survived virtually unchanged for so long when so much has changed around it? This was especially intriguing, and somewhat perplexing to the ACEP scientists, as the studies of the Fricke team[28–31,39,40] point to coelacanths having narrow habitat tolerance and stenotopic phenotypes, which are characteristics expected of species groups (clades) prone to rapid speciation, short, rather than long, species life expectancies and a high probability of extinction.[24,25] If *Latimeria chalumnae* is a stenotope, as the data from the Comoros suggest, then coelacanths are a high profile, unique exception to the rule and call into question the 'Effect Hypothesis'.[24,25] Alternatively, the data regarding the coelacanth's position on the stenotopic–eurytopic continuum may be less robust than initially assumed. As the work of ACEP and other research has progressed, so increasingly evidence is accumulating which indicates that coelacanths are not as narrowly stenotopic as the Comoran data suggested. Coelacanths are more broadly distributed than originally thought, their tolerance range of different structural habitats is broader than one might conclude from Comoran data alone, they seem more tolerant of temperature, light and depth than originally perceived and, while there are expectations that they need oxygen-rich waters, there is also evidence for lower oxygen tolerance. Those data obtained from South Africa, Mozambique, Madagascar, Tanzania, Kenya and also Indonesia, where coelacanths were found in erosion caves and broken areas of boulders which offered protection, suggest that the lava caves of the Comoros are the exception, rather than the norm. In common everywhere, however, is the need for coelacanths to use shelter during the day and, while their ability to cope in currents may be greater than first imagined, they do need to conserve energy. In the Greater St Lucia Wetland Park the demersal habitat of coelacanths is virtually free of current, despite the strong Agulhas Current that dominates the surface waters.

Data from the Comoros, which indicated that coelacanths live in deep cool water, led to an initial expectation that *Latimeria* in the canyons would be numerous, assuming that those found in the shallow canyon heads were representative of a deeper, more extensive population. Data indicate, however, that *Latimeria* is confined to the narrow belt (90–140 m depth) where caves and broken areas offering shelter are abundant. It seems that even though currents in the canyons are absent or slight, the shelter is necessary, suggesting that coelacanths may use caves for protection. The *Jago* team have found scars from what appeared to be encounters with sharks on some specimens in the Comoros. Another possible reason for the existence of coelacanths in the shallow heads of the canyons, rather than deeper down, is that the fish upon which they might prey are more abundant in the canyon heads.[18,20,21]

Conservation and capture of coelacanths

Increasing numbers of coelacanths have been located in a growing geographic area in recent years. This is due in large measure to deep gill nets being placed in coelacanth habitats, which was not previously the case. It is also due to a greater awareness of the significance of coelacanths, which means catches that might have gone unnoticed previously are now brought to the attention of authorities. Nowhere, however, is there an indication that coelacanths exist in large colonies. Therefore, any moves to reduce their status from Appendix 1 on the CITES list of endangered species would be premature. Indeed, the proposals to develop Marine Protected Areas in several countries to protect *Latimeria chalumnae* are welcome.

For many years a variety of organizations have been keen to capture coelacanths so that they might be placed within aquaria to promote understanding, including conservation measures. This issue was debated at the conference too. It was resolved, however, that no attempt to capture coelacanths should be sanctioned given present knowledge of their population size and physiological sensitivities. To endeavour to capture a coelacanth and to fail to keep it alive would impede achievement of the conservation goals to which all aspire.

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