Coelacanth discoveries in Madagascar, with recommendations on research and conservation

The presence of populations of the Western Indian Ocean coelacanth (Latimeria chalumnae) in Madagascar is not surprising considering the vast range of habitats which the ancient island offers. The discovery of a substantial population of coelacanths through handline fishing on the steep volcanic slopes of Comoros archipelago initially provided an important source of museum specimens and was the main focus of coelacanth research for almost 40 years. The advent of deep-set gillnets, or jarifa, for catching sharks, driven by the demand for shark fins and oil from China in the mid- to late 1980s, resulted in an explosion of coelacanth captures in Madagascar and other countries in the Western Indian Ocean. We review coelacanth catches in Madagascar and present evidence for the existence of one or more populations of L. chalumnae distributed along about 1000 km of the southern and western coasts of the island. We also hypothesise that coelacanths are likely to occur around the whole continental margin of Madagascar, making it the epicentre of coelacanth distribution in the Western Indian Ocean and the likely progenitor of the younger Comoros coelacanth population. Finally, we discuss the importance and vulnerability of the population of coelacanths inhabiting the submarine slopes of the Onilahy canyon in southwest Madagascar and make recommendations for further research and conservation.

Significance:

- The paper contributes significantly to knowledge of the distribution and ecology of the Indian Ocean coelacanth, Latimeria chalumnae.
- The paper provides the first comprehensive account of Madagascar coelacanths and demonstrates the existence of a regionally important population and extensive suitable habitat, correcting an earlier hypothesis that coelacanths in southwest Madagascar were strays from the Comoros.
- The results have application in the study of the evolution, biology, ecology and conservation of the species.
- The significant threat posed by gillnet fishing to coelacanths and other species is highlighted as are the negative effects of the shark-fin trade.
- The paper emphasises the importance of the Onilahy marine canyon in southwest Madagascar as an especially important habitat and provides the basis for the development of a national programme of research and conservation.

Introduction

When a living coelacanth was caught off the coast of South Africa in December 1938 it caused an international sensation. J.L.B. Smith named the new species Latimeria chalumnae1 and predicted2 that it was a stray from warmer rocky reefs in the tropical Western Indian Ocean. Over the next 14 years, Smith and his wife Margaret scoured the coasts of Mozambique, Tanzania and Kenya looking for coelacanths but also collecting other fishes. Their searches were confined to the mainland coast and to islands near the coast as they did not have the resources to explore the Comoros or Madagascar. Eventually a coelacanth caught by a traditional fisher off Anjouan (Nzwani) island in the Comoros in December 1952 was brought to Smith’s attention3 and, in one of the most remarkable episodes in the history of ichthyology, he rushed to fetch “his” fish from a foreign country in a South African military aeroplane4,5.

The French government, which held sovereignty over the Comoros and Madagascar at the time, was piqued at Smith’s “fishjacking” and banned research on the coelacanth (and other fishes) by foreign scientists in the Comoros; this ban lasted until the Comoros (except Mayotte) declared independence from France in 1975. A third coelacanth was caught off Anjouan Island in the Comoros in 19536 and a further six specimens off Grande Comore or Anjouan in 19547,8. All these specimens, except one which was lost, as well as the next 15 specimens, all caught in the Comoros, were acquired by French scientists and lodged in the Museum National d’Histoire Naturelle in Paris and in other French museums. Thereafter, coelacanth specimens were sent to other museums, although by far the largest number of holdings is in museums in France (45 specimens by 2011)4.2,8.

Early coelacanth research in Madagascar

In 1947, Jacques Millot, a French scientist based in Madagascar, was appointed as director of the Institut Scientifique de Madagascar. In 1948, he became president of the Académie Malgache and, in 1952, was placed in charge of French research on the coelacanth. The third coelacanth caught off Anjouan in 1953 was transported by air to the Tsimbazaza Museum in Antananarivo where it was examined and described in detail by Millot9 in Naturalista Malgache. This specimen is currently on display in the Department of Animal Biology at the University of Antananarivo. Millot9 was also the first scientist to examine a live coelacanth when he briefly observed a dying female which had been caught in November 1954 and placed in a sunken boat in Mutsumudu, where it survived for over 19 hours. Madagascar therefore played an important role in early coelacanth research.
Fossil coelacanths

Fossils of extinct coelacanths have been known from Madagascar for over 100 years. *Coelacanthus madagascariensis* was described by Woodward in 1910, *Whiteia wardi* and *W. tuberculatae* by Moy-Thomas in 1935 and *Piveteauia madagascariensis* by Lehman in 1952, all from Lower Triassic deposits. The African mainland has also yielded an abundance of fossil coelacanths from both coastal and inland localities as many extinct coelacanths lived in fresh waters. Fossil coelacanth discoveries have been made in the Congo, Egypt, Morocco, Niger, South Africa, Zaïre (now the Democratic Republic of the Congo) and Zimbabwe.

Distribution of living coelacanths

The distribution of *L. chalumnae* includes South Africa (first recorded in 1938), Comoros (1952), Madagascar (1987), Mozambique (1991), Kenya (2001) and Tanzania (2003). The recent sighting of a live *L. chalumnae* off the south coast of KwaZulu-Natal, 325 km south of the iSimangaliso Wetland Park where the main South African population is located, suggests that *L. chalumnae* is more widespread along the South African coast than previously thought and that the first specimen caught off East London may not have been a stray. Another species of living coelacanth, *L. menadoensis*, has been found off Indonesia.

Although the terrestrial fauna of Madagascar is characterised by high levels of endemism, with 84% of land vertebrates being endemic due to its long separation from the African continent since the splitting of the supercontinent Gondwana 88 million years ago, its marine fauna is essentially continuous with the marine life of the east coast of Africa and other Western Indian Ocean islands and shows much lower levels of endemism than its terrestrial biota.

Coelacanth inventory

Since 1972, an inventory of all *Latimeria* specimens known to science has been compiled and maintained in an internationally collaborative effort. Through the Coelacanth Conservation Council/Conseil pour la Conservation du Coelacanthe (CCC), established in 1987, CCC numbers have been allocated to all *Latimeria* specimens. To date (May 2020), 334 coelacanth captures have been documented, making it one of the most comprehensive inventories of all the known specimens of a species ever compiled.

In addition to the inventory of dead coelacanth specimens, H. Fricke and his team have compiled an inventory of 68 individual live *L. chalumnae* which they have observed over a 21-year period off Grande Comore Island in the Comoros. Fricke and the African Coelacanth Ecosystem Programme team have also compiled an inventory of 32 individuals in South Africa in the iSimangaliso Wetland Park in KwaZulu-Natal. As all living coelacanths have unique patterns of white spots on their bodies, which are effectively ‘individual fingerprints’, individuals can be distinguished visually from one another by divers.

Live coelacanths caught off Madagascar

In his book *Old Fourlegs*, J.L.B. Smith predicted that coelacanths live off Madagascar. ‘There must be stretches of coast there that no enlightened scientific eye has ever seen’, and even suggested that local people ‘feasting unsuspected on succulent coelacanth steaks on a Madagascan shore did not seem too fantastic’.

In 1969, 28-year-old Hans Fricke, who would later become the most distinguished researcher on the living coelacanth, visited Madagascar to study the fish in its natural environment. During his initial scuba dives to a depth of 85 m off Nosy Iranja, a small island in northwest Madagascar, he did not find any coelacanths (Nosy Iranja and nearby Ankazoberavina Islands are now part of the Ankivonjo Marine Protected Area and the nearby drop-offs are potential coelacanth habitats). When Fricke returned to the Western Indian Ocean in 1987 with a research submarine, he chose to dive off Grande Comore (Ngazidja) in the Comoros where he and his team carried out a detailed study of the living coelacanth in its natural habitat and proclaimed the Comoros to be the home of the coelacanth.

Although coelacanths may have been caught previously by fishers off Madagascar, at least since the arrival of gillnets in the 1980s, the first specimen caught off the island which was known to Western scientists until recently (CCC 173) was landed off St Augustin, south of Toliara, on 5 August 1995. This specimen was bought by Dominque Coutin from fishers for USD6.00 and taken by boat to Toliara. However, an earlier specimen (CCC 300) has recently come to our attention which was caught in 1987 off Anakao in southwest Madagascar (Table 1, Figure 1). This specimen is on display in the Museo Civico di Storia Naturale in Como, Italy, and is described by Inascco et al. Since then, at least 32 additional specimens known to science have been landed off Madagascar, although others have been caught but lost. Sufficient coelacanths have been caught in Madagascar for it to have a common name. In the Toliara area it is known as *fiandrolo* (‘ghost fish’). It is called *gombessa* (‘taboo’) in the Comoros and the Indonesian species is known as *raja laut* (‘king of the sea’).

In their 1996 paper, Heemstra et al. surmise that the 1995 specimen caught in Madagascar (CCC 173) was most likely a stray from the Comoros population, based on fishers’ lack of local knowledge of the coelacanth and the genetic similarity of the pups with the Comoros population. We argue that the coelacanth populations in Madagascar are ancestral to those in the Comoros and that Comorian coelacanths are the descendants of those in Madagascar. We go beyond Hans Fricke and reinforce Green et al. in predicting that coelacanths are likely to be distributed around the entire coast of Madagascar and that, with its >5000-km coastline, Madagascar is likely to harbour the largest populations of coelacanths in the Western Indian Ocean.

Inventory of coelacanths caught off Madagascar

The inventory of coelacanth specimens caught off Madagascar has been updated using data from the official CCC Coelacanth Inventory, and subsequent updates have been made from supplementary information collected on coelacanth specimens during a survey in Madagascar in November 2019 by one of the authors (M.R.) under the auspices of the consultancy company Resolve sarl in collaboration with Clemence Ravelo from the Institut Halieutique et des Sciences Marines (IHSM) at the University of Toliara, and from other publications.

During the survey, meetings were held with the director of the IHSM, Dr Jamal Mahafina, representatives of the fishing companies Coperfrito and Murex, staff of the Regional Fisheries Directorate in Toliara, staff of the Jardin de la Mer in Toliara, and with Mr Tinard, an experienced fisherman. Frozen, formalin-preserved and dried coelacanths in various locations were also photographed during this survey. Specimens CCC 251 (Figure 2) and 317 (Figure 3) were photographed and credited to D. Stanwell-Smith and T. Cordenos, respectively.
The 34 specimens known to have been caught in Madagascar are listed in Table 1; further details on these specimens are available online at https://www.resolve.mg/download/MadagascarCoelacanthInventory_23Sept2020.pdf. The surviving specimens (or parts thereof) are currently located in a variety of institutions and locations including museums, universities, commercial fishing companies (Copefrito and Murex, both in Toliara), the Résidence Eden Ecologique, the Jardin de la Mer (an exhibition centre on Malagasy plants and animals in Toliara), NGOs and the regional fisheries directorate of Toliara. One specimen (CCC 176) is on display in the Tolagnaro (Fort Dauphin) Town Hall.

Location of captures

Capture locations where known are shown on bathymetric maps of western and southern Madagascar (Figure 4) and off the Onilahy River mouth, Toliara, in southwest Madagascar (Figure 5). Capture points are approximate and represent the best estimate of capture location based on available information on depth, distance and direction from any reference point and the location of other captures by fishers from the same village. The captures were made over a wide geographical range extending from 80 km to the southwest of Cap Ste Marie, the southernmost point of Madagascar, as far north as three sites near Maintirano in northwest Madagascar (590 km to the north of Toliara) – a range of almost 1000 km. Of the 34 specimens, 21 form a cluster in southwestern Madagascar in the vicinity of the Onilahy canyon (Anakao, Lovekampy, Soalara, Nosy Ve, St Augustine, Andranona and Sarodran); Figure 5). Nonetheless, the capture of coelacanths at Fihenemasy and Tsandamba, respectively 40 km and 85 km north of Toliara (Figure 4) where the shelf is narrow and no canyons are present, suggests that their association with undersea canyons is not exclusive; depth and slope may be the primary determinants for the occurrence of coelacanths, as also suggested by Green et al.22

Despite the widespread practice of shark fishing using gillnets set at depths of 100 m or more throughout the island20-31, no coelacanths have as yet been reported from the northwest around Nosy Be or the northernmost point of Madagascar near Antsiranana, which is just 652 km from the Comoros. There are also no coelacanth records from the east coast of Madagascar, despite the presence there of a steeply shelving continental slope and at least one undersea canyon (at Maningory, south of Ille Ste Marie), although this may be an artefact of the much lower levels of fishing effort there and the absence of sailing pirogues capable of reaching the continental slope. Further research is necessary to ascertain whether coelacanths do live in these unexplored areas along the east coast.

The distance from shore at which coelacanths were estimated to have been caught off Madagascar, all along the west coast, ranged from 0.8 km to 80 km (average 9 km), which is further offshore than in Grande Comore (where 85% of coelacanths are caught less than 1.5 km from shore20,31) and Tanzania (average 6.9 km, range 0.5–8 km)34. The wide range of distance from shore at which coelacanths have been caught in Madagascar corresponds with the widely varying width of the continental shelf, which is as narrow as 1 km at St Augustin in the south, where most captures have been recorded, extending to over 100 km off Cape St André in the west. The estimated depth of capture in Madagascar ranged from 60 m to 500 m (average 191 m), shallower than in the Comoros20,33 but deeper than in Tanzania (average 141 m, range 50–250 m15).

Madagascar originally occupied a landlocked position at the centre of Gondwana until the supercontinent began to break up about 160 million years ago. About 88 million years ago, India split off from Madagascar, moving northwards to join Asia. Madagascar then shifted more slowly northwards to its current isolated position in the Western Indian Ocean about 40 million years ago, since when it has experienced relatively stable climatic and oceanographic conditions.34 This can be compared with the young Comoro islands whose ages range from 15–10 million years (Mayotte) to just 130 000 years (Grande Comore).30 It is likely that either Madagascar or the African mainland represent the more ancestral habitat of coelacanths before they colonised the Comoros in relatively recent geological time, but this proposal needs to be tested using genetic evidence. DNA studies on coelacanths that have previously been caught in Madagascar would have to be carried out on the frozen specimens as all the dried and formalin-preserved specimens have been exposed to formalin.

The Pleistocene (which started about 2.6 million years BP), when sea levels dropped by 100 m or more, and when Madagascar’s major rivers would have cascaded off cliffs and down steep slopes into the sea.35 The closest of these canyons to the existing shoreline is the Onilahy canyon, site of most coelacanth captures to date, but other deep canyons also exist on the east coast.22,37 Furthermore, Madagascar’s southwestern and eastern continental margins are steeply shelving, potentially providing 2000–3000 km of suitable habitat for coelacanths, as suggested by Green et al.22

Figure 2: Coelacanth CCC 251 caught in March 2001 at Fihenemasy and now in the collection of the IHSM Museum, Toliara (photo provided by D. Stanwell-Smith).

Figure 3: Coelacanth CCC 317 caught on 13 May 2010 at Nosy Ve, identified by IHSM Museum staff, and sold in the market at Toliara (photo: T. Cordenos).
### Table 1: Information on the coelacanths known to science caught in Madagascar between 1987 and 2019. Additional information on these specimens is given in the text and full details are given in Cooke et al.28

| No. | CCC number | Date of capture | Site of capture | Distance from shore (km) | Depth of capture (m) | Weight (kg) | Length (cm) | Sex | No. of eggs | No. of pups | Fishing gear | Current holding |
|-----|------------|----------------|----------------|-------------------------|---------------------|-------------|-------------|-----|-------------|-------------|--------------|-----------------|
| 1   | 300        | 1987           | St Augustin    | nd                      | 30-35               | 121         | M           | nd |             |             |             | MCSN            |
| 2   | 173        | 03.08.1995     | Onilahy       | 4–9                     | <190                | 34.98       |             | M              |             |             | Jarifa          |
| 3   | 176        | 06.12.1997     | Onilahy       | 2–3                     | 60                  | 190         | F           | 13             |             |             | Tolagnaro Town Hall |
| 4   | 177        | 03.03.2001     | Fiherenamasay | 3–4                     | 100                 | 75          | F           | 9              |             |             | Jarifa          |
| 5   | 179        | 21.07.2001     | Tsiandamba    | 5–6                     | >100                | 73          | F           | 4              |             |             | Jarifa          |
| 6   | 205        | 18.05.2006     | Nosy Lava     | Nd                      | 140                 | 171         | F           | 6              |             |             | IHSM            |
| 7   | 231        | 18.02.2009     | Fiherenamasay | Nd                      | 200                 | 110         | M           | 11             |             |             | Jarifa          |
| 8   | 232        | July 2002      | Toliara       | nd                      | nd                  | 150         | F           | 4              |             |             | Jarifa          |
| 9   | 244        | 20.09.2008     | Cap Ste Marie | 80                      | nd                  | 150         | F           | 9              |             |             | Jarifa          |
| 10  | 245        | April 2008     | Maintirano    | nd                      | nd                  | nd          | F           | 2              |             |             | Jarifa          |
| 11  | 251        | 22–29.03.2001  | Fiherenamasay | nd                      | 120                 | 180         | F           | 2              |             |             | IHSM            |
| 12  | 252        | 12.07.2005     | Fiherenamasay | nd                      | nd                  | 60.3        | F           | 2              |             |             | Jarifa          |
| 13  | 284        | 22–23.09.2010  | W of Nosy Ve  | >2                      | >150                | 85          | F           | 2              |             |             | Jarifa          |
| 14  | 285        | 27.11.2010     | W of Nosy Ve  | 1–2                     | 250                 | 134         | M           | 3              |             |             | Jarifa          |
| 15  | 310        | April 2011     | Onilahy Canyon| nd                      | >300                | nd          | F           | 2              |             |             | Not kept       |
| 16  | 288        | 5 May 2010     | W of Nosy Ve  | >1                      | 150                 | nd          | F           | 2              |             |             | Jarifa          |
| 17  | 289        | 10.02.2011     | W of Nosy Ve  | 20                      | 200                 | 80          | 175         | F              |             |             | Jarifa          |
| 18  | 290        | 11.02.2011     | W of Nosy Ve  | 2                       | 200–300             | 60          | 149         | F              |             |             | Jarifa          |
| 19  | 291        | 13.02.2011     | NW Sarodrano  | 7                       | 200–300             | 75          | 170         | F              |             |             | Jarifa          |
| 20  | 292        | 12.03.2011     | NW Sarodrano  | 3                       | 200–300             | 75.2        | 182         | F              |             |             | Jarifa          |
| 21  | 293        | 21.05.2011     | W of Nosy Ve  | 2                       | 150–200             | 29.45       | 130         | M              |             |             | Jarifa          |
| 22  | 294        | 02.07.2011     | Andanora      | 7                       | 150–200             | 84.64       | 170         | F              |             |             | Jarifa          |
| 23  | 295        | 03.08.2011     | W of Nosy Ve  | 10                      | 150–200             | 32          | 140         | F              |             |             | Jarifa          |
| 24  | 296        | 25.08.2011     | W of Nosy Ve  | 2                       | 150–200             | 62          | 170         | F              |             |             | Jarifa          |
| 25  | 297        | Jan 2012       | St Augustin   | nd                      | nd                  | nd          | nd          | nd             |             |             | Jarifa          |
| 26  | 311        | 31.05.2012     | Fiherenamasay | nd                      | 100–200             | 36          | F           | 2              |             |             | Jarifa          |
| 27  | 298        | July 2012      | Toliara       | nd                      | nd                  | nd          | Very large  | F              |             |             | Jarifa          |
| 28  | 312        | 2012           | Maintirano    | nd                      | 100–200             | 36          | nd          | nd             |             |             | Jarifa          |
| 29  | 301        | Feb 2013       | Ambanilia     | 6                       | 500                 | 35          | 130         | M              |             |             | Eden Ecolodge  |
| 30  | 313        | Feb 2013       | St Augustin   | nd                      | nd                  | 35–50       | 150         | M              |             |             | Jarifa          |
| 31  | 314        | 2015           | Anakao        | nd                      | nd                  | nd          | nd          | nd             |             |             | Jarin de la Mer|
| 32  | 315        | 11.06.2011     | Toliara       | nd                      | nd                  | nd          | nd          | nd             |             |             | DRAEP           |
| 33  | 316        | 23.03.2019     | Barnhill Point| 0.8–1                  | 200                 | 79          | 150         | F              |             |             | DRAEP           |
| 34  | 317        | 13.05.2010     | W of Nosy Ve  | nd                      | nd                  | nd          | nd          | nd             |             |             | Jarifa          |

Sources: Bruton and Coutouvidis,7 Nulens et al.8 Heemstra et al.11, Insacco et al.12, Ravobeloharirejara13, Vicente14, Naina15, Anon16, Houssen17 and personal communications as indicated in the text.

Holdings: Copefrito, Compagnie de Pêche Frigorifique de Toliara fishing company, Toliara; DRAEP, Direction Régionale de l’Agriculture, de l’Elevage et de la Pêche, Toliara; Eden Ecolodge, Eden Ecolodge, Sarodrano; IHSM, Institut Halieutique et des Sciences Marines, University of Toliara; MCSN, Museo Civico di Storia Naturale, Comiso, Italy; MNHN, Muséum National d’Histoire Naturelle, Paris, France; Murex, Murex International fishing company, Toliara

Jarifa, large-mesh gillnet laid for sharks

nd, no data
Figure 4: Map showing the location of captures from 1987 to 2019 of all coelacanths in Madagascar whose capture location is known.
Figure 5: Map of St Augustin Bay, southwestern Madagascar showing the locations of the cluster of coelacanths caught from 1987 to 2019 near the Onilahy canyon.
Along the west coast, near the Onilahy canyon, the continental shelf is very narrow. Northwards from the Manombo River, the shelf broadens and suitable habitats for coelacanths at depths of 150 m or more are typically found far offshore, such as off the Barren Islands, to the west of Maintirano, where migrant zvoo fishers regularly establish seasonal camps about 40 km offshore of the main island. In contrast, on Grande Comore, a young island with an active volcano (Karthala), the shores are steep sloping and deep water can be reached within a few hundred metres from shore using wooden dugouts (galawa). Handline fisheries, to which coelacanths are vulnerable, are therefore better developed in the Comoros than in Madagascar.11,23,40

Capture frequency, seasonality and demography

Many coelacanths, other than those recorded in Table 1, are likely to have been caught by artisanal fishers in Madagascar. In December 1998, a commercial fishing crew was reported to have caught a female coelacanth (180 cm, 85 kg) off Toliara which contained seven embryos, but the specimen was not kept nor authenticated.41 An experienced fisherman, Mr Tinard, from Lovokampy and his team were reported to have caught ‘dozens of coelacanths in a single week, but they were all consumed’ in 201043 and none was documented. In 2016, Tinard caught another undocumented coelacanth and, in May 2016, he landed a small female and found ‘a few small coelacanths in the belly’. He also reported to Raveloloharinaraja27 that his family did not use jarifa gillnets in 2018 and caught no coelacanths in that year. Another fisherman, Tine Hoe Julien, is reported to have caught seven coelacanths off Nosy Ve, Sarodrano and Andanora between May 2010 and July 2011.23

Coelacanth catches were made in every month of the year in Madagascar except October, with most catches in February (6), May and July (5) and March (4), although the sample size (31) for which the month of capture is known is too small to show real trends. In the Comoros, coelacanth catches were also made throughout the year with a peak from November to March12,24, whereas catches peaked in September (21%) and August (17%) in Tanzania15. All coelacanth captures in Madagascar for which the capture method is known (23) were made using deep-set jarifa gillnets targeting sharks19,23 (Table 1). In the Comoros, all coelacanth catches were made using handlines until the arrival of gillnets in the 1990s.33 In Tanzania, 35 (87.5%) of the 40 coelacanths for which the capture method is known between 2003 and 2015 were caught using 15-cm jarifa gillnets except for two caught on handlines, two moribund specimens found floating on the water surface and one caught in a ring net.8,15

The coelacanths caught in Madagascar which were measured ranged in weight from 29.45 kg to 90 kg (average 57.2 kg) and length from 121 cm to 190 cm (average 156.9 cm; Table 1), equivalent to the weight range is wider.4,15 Although aspects of the demography of coelacanths in Madagascar, the Comoros and the African mainland differ, these differences are more likely to be a function of the different fishing methods that are used, and the different locations and depths that are fished, rather than representing discrete demographic groups of coelacanths, but this supposition needs to be tested using genetic evidence. Such evidence could also be used to determine whether gene flows exist between the different coelacanth populations and to support or reject the hypothesis that Madagascar or the African mainland is the ancestral home of coelacanths on the basis that older (and larger) populations would be expected to have higher genetic diversity. Studies carried out so far suggest that coelacanths in the Western Indian Ocean share very similar genetic material.7,17,41

Threat of jarifa gillnets

Sharks have been targeted by artisanal fishers for shark fin and oil in the Western Indian Ocean for more than a century. Petit12 found that shark fishing and shark fin exports from Madagascar were already established by 1900 and Schaeffer43 reports that shark fin exports started as early as 1919 and that 6.6 tons of shark fins had been exported from Zanzibar by 1923. Shark fishing intensified significantly with the rapid growth of the Chinese economy in the 1980s and the resulting demand for shark fin and continues today.20,44,45

Shark meat is widely eaten by fishing communities in Zanzibar3,46 and Madagascar46, although it is not as prized as the flesh of bony fish. A benefit of shark meat to rural people is that it preserves well unrefrigerated when it has been dried and salted but shark meat consumption and export are sometimes discouraged due to the risk of poisoning caused by toxicity originating from dinoflagellates.28

The jarifa gillnets used to catch sharks are a relatively new and more deadly innovation as they are large and can be set in deep water. There are two kinds of jarifa nets: those with large meshes (15 cm or 24 cm stretched mesh) which are often baited with small fish, and those with smaller meshes (10 cm; called ‘22 nets’) which are not baited (Nulens R, personal communication, 9 March 2020). Large-mesh jarifa gillnets are used in Madagascar and Tanzania, with fishers from the former country using 24-cm stretched-mesh nets3 and, from the latter, 15-cm nets11.32

The introduction of market forces from abroad has often resulted in much greater pressure being placed on a natural resource that was once exploited sustainably for local use47 and this appears to be the case in Madagascar. There is little doubt that large mesh jarifa gillnets are now the biggest threat to the survival of coelacanths in Madagascar. The nets are set in deep water, generally between 100 m and 300 m, within the preferred habitat range of coelacanths, and, unlike trawl nets, can be deployed in the rugged, rocky environments which coelacanths prefer. They would be difficult to detect by the fishes as they are static and do not produce a pressure wave like active gear, such as a trawl net. Furthermore, coelacanths hunt at night and have poor eyesight and their main sense organ, electro-reception48, may not be triggered by the thin strands of a gillnet. In fact, coelacanths may be attracted to the nets as they are typically baited with small fish in Madagascar. A significant number of coelacanths has also been caught in jarifa gillnets off Tanga in Tanzania where 19 were caught in 6 months in 2004/2005, including 6 in one night.4,15,46

The incidental capture of coelacanths in jarifa gillnets off Madagascar is not a disincentive for shark fishers because of the high scientific interest in the fish which inevitably commands a price, even in the absence of a true market. The presence in Toliara of a marine research institute (HISM) has increased fishers’ awareness of the coelacanth’s significance and value. Baker-Métral and Faber40 report payments of 150 000–400 000 arsat (USD40–110) for coelacanth specimens caught in the Toliara region.

The illegal trafficking of coelacanths may be taking place in Madagascar. When the Centre de Surveillance des Pêches checked the cargo of the factory ship, El Amine, on 20 September 2008, following a tip-off from the Coast Guard, they found an undeclared coelacanth (CCC 244) hidden on board, and several other infringements of the fishing laws were revealed. The El Amine was escorted to Toliara where the coelacanth was handed over to the authorities and stored in the cold room of the factory ship, where it is still housed. On 21 October 2008, the newspaper Les Nouvelles headlined an article on the incident which reported that over 300 kg of coelacanths had been captured by El Amine’s jarifa nets and stating that they suspected that coelacanth trafficking had been taking place. After paying a fine, the El Amine was allowed to leave Toliara on 30 October 2008.

Furthermore, a fish biologist, Dr Faratiana Ratsifandrihamanana, reported to one of us (M.R.) that she had seen a cartful of dead coelacanths in the yard of the IHSM in April 2012. They comprised 4 adults (about 1.5 m in length) and 5–7 juveniles (60–70 cm). These specimens had been caught by fishers from St Augustin who told her that they had been deliberately targeted as they could sell them to vazaha (foreigners) at 100 000 arsat per fish.31 This is clear evidence that fishers can target coelacanths and that there is an informal market for them. The IHSM refused to buy the fish and they were taken away.
Coelacanth discoveries in Madagascar

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The coelacanth bycatch fishery is significant as their populations are unlikely to be able to survive high exploitation rates as they have all the attributes of species that are vulnerable to extinction, including rarity, large size, high trophic level in the food pyramid, low dispersal rates, few offspring, high longevity and high levels of specialisation.3,35 In addition, coelacanth populations may be small. The best studied population is that off Grande Comore where Fricke and his team estimated that the population size in 1990 was no more than 300 adults.36,37 Coelacanths may also be susceptible to capture in the snagging meshes of a gillnet as they have large mouths with sharp teeth, large opercula, eight spines on the first dorsal fin and paired lobed fins.

Gillnets are deadly for another reason – if they are lost or abandoned at sea they continue to catch fishes and shellfishes for months, or even years, as the synthetic fibres from which they are made do not rot quickly. This “ghost fishing” can be very harmful to fish and shellfish stocks.38 Jartila gillnets (in use or lost) are also known to catch dugongs and turtles in Madagascar.39,40 Outside Madagascar, the biggest threats to coelacanths, other than jartila gillnets, are the use of explosives by fishers, recorded in Tanzania and the Comoros, and insecticide residues and plastic litter in the oceans.3,8,15,32,41 The use of explosives has not been reported in Madagascar, whilst the presence of insecticide residues and plastic litter has not been assessed.

Coelacanths as food

The capture of coelacanths as a source of food is hard to justify as its flesh is rancid and contains large amounts of urea, which coelacanth stores in their tissues like esmolbranchs, as well as oils, wax esters and other compounds that are difficult to digest. Madagascar is one of the few places where coelacanth flesh is regularly eaten. Of the 34 specimens listed in Table 1, 10 were sold by fishers at a market or eaten (or used as bait) after they had been documented. Ravololoaharinjara42 was told that a 32-kg male fish (CCC 295) which had been housed in the cold room of the fishing company Murex in Tolitara, had been ‘shared with company personnel during the passage of Cyclone Haruna in 2013’. Coelacanth flesh is occasionally eaten in Tanzania43 and in Anjouan in the Comoros (Fricke H, personal communication, June 2020).

Future coelacanth research

Although most coelacanth specimens known to have been caught in Madagascar have resulted from chance catches by artisanal fishers, who are mainly targeting sharks, rather than from a structured scientific research programme, the available evidence suggests that Madagascar does have a permanent and widespread population of breeding coelacanths. As the coelacanth is such an important species from ecological, conservation and historical perspectives (see below) it makes sense to take advantage of this opportunity to mount a structured international research programme on the species, based not only on chance catches but also on live observations of the fishes in their natural habitat, as has been done in the Comoros, Tanzania and South Africa.

The Madagascan coelacanth programme would build on the African Coelacanth Ecosystem Programme and the former collaboration between this Programme and the Agulhas & Somali Currents Large Marine Ecosystem Programme, linking coelacanth and ocean ecosystem research, of which Madagascar is a participating country. African Coelacanth Ecosystem Programme (and formerly the Agulhas & Somali Currents Large Marine Ecosystem Programme) is based out of the South African Institute for Aquatic Biodiversity.

The most practical scenario for live observations of coelacanths in Madagascar would be to use a remotely operated submersible such as the Sea-Eye owned by the South African Institute for Aquatic Biodiversity which has already been used with great success to document the distribution, abundance and behaviour of coelacanths in the iSimangaliso Wetland Park in Kwazulu-Natal and elsewhere.44 This research could initially focus on determining the distribution, abundance, habitat preferences, depth range and diel activity patterns of coelacanths – information which is needed for their management. The study of dead coelacanths derived from the artisanal fishery can also continue to yield useful information if the collection of data and the preservation of the specimens are carried out professionally. A standardised questionnaire is required which captures as much information as possible (as per the categories in the CCC Coelacanth Inventory) on each caught specimen. This information should then be included in the official inventory and made available to the international community via publications. An awareness campaign among artisanal fishers also needs to be launched to encourage them to share information on their coelacanth catches with the authorities.

Whenever practical, caught coelacanths that are in good condition should be deep frozen rather than preserved in formalin so that tissue samples can be taken for further analyses. The only Madagascan specimen that has so far been subject to detailed tissue analysis is CCC 177 caught in March 2001 which was taken by PC. Heemstra to the J.L.B. Smith Institute of Ichthyology (now South African Institute for Aquatic Biodiversity) in South Africa.45 Samples of scales and of muscle and dorsal fin tissue were used for stable isotope analyses.

It is important that this study is pursued further using genetic methodologies with tissues taken from frozen specimens. At present, this research would have to be performed outside Madagascar as the only DNA analysis machine available (in the capital Antananarivo) can only extract and conduct DNA hybridisation assays but cannot sequence the genome. miDNA and full genome tests would be useful to assess the extent of divergence of coelacanth populations, and the genetic diversity among regional populations, perhaps using the methods adopted in the EDGE programme. Interestingly, genetic research on dugongs has revealed that the Madagascan and Comorian populations of dugongs are genetically distinct from those of the East African coast, which suggests that the Mozambique Channel can be a barrier to the movement of primarily coastal shelf species.46

Coelacanth conservation

Both the Western Indian Ocean coelacanth (L. chalumnae) and the Indonesian coelacanth (L. menadoensis) are listed on Appendix I of CITES (may not be traded for commercial gain). L. chalumnae is rated as ‘Critically endangered’ by the IUCN (very highly vulnerable to extinction) and L. menadoensis as ‘Vulnerable’. The two living coelacanths may also be considered ‘EDGE species’ (Evolutionarily Distinct and Globally Endangered) which have a high global conservation priority due to the significant level of unique evolutionary history that they embody. Considering the international significance of L. chalumnae, and the fact that Madagascar is one of only four countries known to host breeding populations (with the Comoros, South Africa and Tanzania), although single specimens have so far been caught off Mozambique47 and Kenya48, it is very important for Madagascar to contribute to the conservation of the coelacanth.

The exact conservation status of coelacanths in Madagascar cannot be determined until we have better information on their distribution and population densities around the entire island. If coelacanths occur around the whole coast, as we predict, then the total population could be regarded as stable as the catches made on the southwest and west coasts, even if several times greater than the documented rate (about one per year for 33 years) would probably be trivial in relation to the size of the population. However, we have anecdotal evidence that ‘dozens more’ coelacanths have been caught off southwest Madagascar in recent years compared to the number that has been officially recorded,36 so the true catch rate may be substantial. If coelacanths are only found at or near the currently known sites, or at only a small number of other sites, then there would be reason for concern.

The results of demographic studies on coelacanth populations off Grande Comores and Anjouan islands in the Comoros demonstrate that the known catch rates of 3.5 fish per year in the 1960s, 1970s and 1980s were insignificant compared to natural mortality rates that were calculated to be between 137 and 174 individuals per annum. The main source of natural mortality was considered to be predation by sharks.49
A worrying trend in coelacanth catches in Madagascar is the relatively high proportion of pregnant females which is landed. The breeding mode of coelacanths – a very long gestation period (36 months) with the live bearing of a few, very large young (33 cm, 500 grams) rather than the production of a large number of small eggs as in most teleost fishes – means that they invest a large amount of energy in each of a few young. Killing of pregnant females carrying eggs or unborn pups is therefore a major setback for the population. There is evidence from Madagascar and other localities that pregnant coelacanths may be relatively vulnerable to gillnet and trawl net catches.

Of the 22 coelacanths caught off Madagascar whose sex is known, only 5 were male and 17 (77%) female; 5 of the 15 female individuals (33%) carried eggs and/or unborn pups. Of the 26 coelacanths caught off Tanzania between 2003 and 2015 for which the sex is known, 10 were male and 16 (61.5%) were female; half of the 16 female individuals caught were carrying eggs or unborn pups. The only coelacanth caught so far off Mozambique (CCC 162) was a 98-kg, 179-cm female fish carrying 26 late-term pups which was landed using a trawl net. The only coelacanth known from Kenya (CCC 178) was a 77-kg, 170-cm female individual carrying 17 eggs caught in a trawl net in April 2001. An 86.5-kg, 176-cm female coelacanth caught in a net off Unguja Island, Zanzibar, Tanzania, in July 2009 (CCC 253) was carrying 23 fully developed juveniles. It is important to note that over 90% of all coelacanths larger than 50 kg are female and that these larger female fish may be more susceptible than the smaller male fish to capture by large-mesh gillnets set for sharks. The continued capture of pregnant female coelacanths in Madagascar and elsewhere is a serious concern as Frickle et al. have estimated that they produce only 140 young during their entire life cycle.

Although it is tempting, from the perspective of the conservation of the whole marine megafauna, especially sawfish, sharks, coelacanths, turtles, dugongs and dolphins, to call for a complete ban on the importation, transport, manufacture, sale and/or use of jarifa gillnets in Madagascar, such a ban would have wide socio-economic implications for the many people who rely on marine resources for their livelihood. It is therefore necessary to include the human dimension into conservation recommendations, otherwise these recommendations would be ignored and/or the fishing activities would be carried out illicitly. Instead, the use of jarifa gillnets in fisheries management areas and marine protected areas should be strictly controlled and their use should be restricted to areas where they do not pose a significant threat to threatened species.

Coelacanth conservation measures which should be introduced in Madagascar include:

- Passing legislation adding L. chalumnae to the list of integrally protected species under Madagascar’s wildlife laws, which forbid the capture, holding, transport or sale of such species.
- Establishing a strictly protected coelacanth sanctuary in the Onilahy canyon near Anakao where the highest concentration of coelacanths in Madagascar is known to occur. (In Tanzania the Tanga Coelacanth Marine Park has been established along 100 km of coastline from the Pangani River estuary to Mafuruko village north of Tanga City but jarifa gillnets continue to be used in this marine reserve, which results in mortalities to coelacanths and other marine life.)
- Extending or reinforcing marine protected areas, or areas under regional fisheries management plans, where coelacanth populations occur. In these areas, bottom fishing with demersal jarifa gillnets or longlines should be banned, although controlled pelagic fishing could continue, as in the Isimangaliso Wetland Park in KwaZulu-Natal.
- Continuing to enforce a strict ban on the export of coelacanth specimens or body parts in accordance with CITES regulations.
- Implementing an awareness raising campaign targeting fishing communities in areas where coelacanths may occur to discourage their capture.
- Providing incentives for fishers to release caught coelacanths which are still alive, as in the Comoros. The option of tagging and photographing caught coelacanths, in collaboration with registered fishers, in return for an incentive payment, should also be considered.
- Examining, more broadly, the pros and cons of allowing the continuation of the shark fishery using jarifa gillnets by assessing its impact on other artisanal fisheries and on threatened marine megafauna such as sawfish, coelacanths, turtles and dugongs. This assessment should take account of the ecological roles of these species.
- Continuing to mount a nationwide public awareness campaign, including displays, media releases, TV and radio interviews, public talks, talks at schools, and popular publications, on the importance of conserving the coelacanth to build its value as an iconic species.
- Encouraging traditional leaders to support coelacanth conservation, taking inspiration from the venerated status which the species already enjoys in the migrant voo fishing culture.
- Encouraging museums, zoological gardens, research institutions and tourism facilities to mount new and improved displays on the coelacanth in ecological dioramas, using accurate fibreglass replicas rather than real specimens, which are scientifically valuable and deteriorate under display conditions.
- Further developing the genetics laboratory at the University of Antananarivo so that the genomes of coelacanths and other endangered Madagascan species can be sequenced.
- Encouraging the Madagascar government to develop a National Strategy for the Conservation of the Coelacanth in consultation with scientists and natural resource managers and to implement the recommended conservation actions in terms of this National Strategy.
- Recommending that the Madagascar government should use the coelacanth as a flagship for marine conservation.

Conclusions

L. chalumnae is highly significant from several points of view. It belongs to an ancient group of fishes whose origins can be traced back 420 million years and which was close to the important evolutionary transition from water onto land around 320 million years ago. The survival of living coelacanths has therefore provided a unique window into the past. Their enormously long longevity; ability to survive four major extinction events over hundreds of millions of years; early adoption of advanced life-history traits such as live bearing; an extraordinarily long gestation period; unusual swimming, feeding, hunting and social behaviour; and their unique combination of physiological and anatomical characters, some of which they share with bony and cartilaginous fishes and others with tetrapods, set them apart from all other animals. They are among the most valuable animals on the planet due to the unique messages about the past which they carry in their DNA.

Coelacanths have also played a key role in promoting public understanding of the theory of evolution and have become important flagship species for science. Coelacanths also have a rich symbolic history, probably more than any other fish. Their iconic image has been adopted by institutions, artists and craftspeople and has appeared on money and postage stamps. They are the emblem of the Department of Animal Biology, University of Antananarivo, and the mascot of the Comorian national football team. Their phoenix-like ‘resurrection’ from the past has inspired poetry, prose, songs, films, figures of speech and political metaphors. They may be among the most valuable animals on the planet due to the unique messages about the past which they carry in their DNA.

Madagascar may have the largest population of L. chalumnae in the world, much of it still to be discovered. Madagascar also has a research infrastructure comparable to other Western Indian Ocean countries which harbour coelacanth populations and an historical connection to coelacanth research. It is therefore appropriate that Madagascar should
play a key role in marine research and conservation, not only for the coelacanth, but also for the entire ecosystem which they share with other marine organisms.

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Competing interests

We declare that there are no competing interests.

Authors’ contributions

A.C. was responsible for project leadership and management and contributed to conceptualisation, methodology, sample analysis, data analysis, validation and writing the initial draft and subsequent revisions. M.N.B. took the lead with the drafting of the initial manuscript and contributed to the conceptualisation, methodology, data collection, sample and data analysis, validation, data curation and the writing of revisions. M.R. conducted the field survey and contributed to data collection and sample analysis.

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