Coelacanth discoveries in Madagascar, with recommendations on research and conservation

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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 chalumnae*[1] and predicted[2] 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.[2,3] 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 attention[4] 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 aeroplane[2,5].

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 1953[6] and a further six specimens off Grande Comore or Anjouan in 1954[7,8]. 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[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 Millot[6] in *Naturaliste Malgache*. This specimen is currently on display in the Department of Animal Biology at the University of Antananarivo. Millot[9] 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 Mutsamudu, 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 madagascariense* was described by Woodward in 1910, *Whiteia woodwardi* and *W. tuberculatae* by Moy-Thomas in 1935 and *Piveteauia madagascariensis* by Lehman in 1952, all from Lower Triassic deposits.[10] 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, Zaire (now the Democratic Republic of the Congo) and Zimbabwe.[10]

Distribution of living coelacanths

The distribution of *L. chalumnae* includes South Africa (first recorded in 1938)[1], Comoros (1952)[4], Madagascar (1987)[11,12], Mozambique (1991)[13], Kenya (2001)[14] and Tanzania (2003)[15]. 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.[16] Another species of living coelacanth, *L. menadoensis*, has been found off Indonesia.[8,17,18]

Although the terrestrial fauna of Madagascar is characterised by high levels of endemism, with 84% of land vertebrates being endemic[19] 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.[7,8] Through the Coelacanth Conservation Council/Conseil pour la Conservation du Coelacanthe (CCC), established in 1987[5], 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.[20] 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.[21] 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'[2], 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 submersible, 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.[20]

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.[11] 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 Comis in Italy, and is described by Insacco et al.[12] 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 *fiandolo* ('ghost fish'). It is called *gombessa* ('taboo') in the Comoros and the Indonesian species is known as *raja laut* ('king of the sea').

Figure 1: Coelacanth CCC 300, the first coelacanth from Madagascar known to science, caught in 1987 in St Augustin Bay and now on display in the Museo Civico di Storia Naturale in Coviso, Italy (photo: Gianni Insacco).

In their 1996 paper, Heemstra et al.[11] 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.[22] 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[8], 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[23], and from other publications[24-27]. During the survey, meetings were held with the director of the IHSM, Dr Jamal Mahafina, representatives of the fishing companies Copefrito 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.

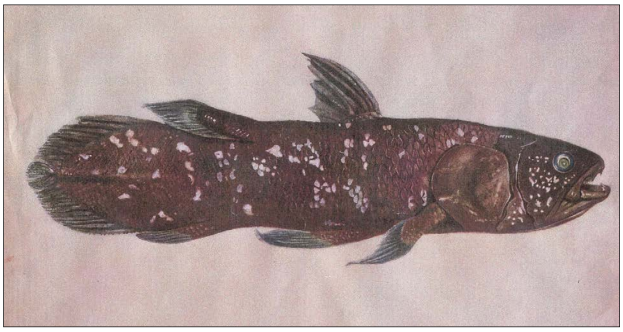

Figure 2: Coelacanth CCC 251 caught in March 2001 at Fiherenemasay and now in the collection of the IHSM Museum, Toliara (photo provided by D. Stanwell-Smith).

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).

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.[28] 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 Ecolodge, 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, Lovokampy, Soalara, Nosy Ve, St Augustin, Andanora and Sarodrano; Figure 5). Nonetheless, the capture of coelacanths at Fiherenamasay and Tsiandamba, 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 island[29-31], 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 Ile 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 shore[32,33]) and Tanzania (average 6.9 km, range 0.5–8 km)[15]. 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 Comoros[8,32,33] but deeper than in Tanzania (average 141 m, range 50–250 m[15]).

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).[35] 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.

Madagascar's ancient continental margin is cut at several locations by deep canyons which were created during previous ice ages including 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.[36] 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]

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	nd	30-35	121	M			nd	MCSN
2	173	03.08.1995	Onilahy	4–9	<190	34.98	134	M			Jarifa	IHSM
3	176	06.12.1997	Onilahy	2–3	60	90	190	F	13		Jarifa	Tolagnaro Town Hall
4	177	03.03.2001	Fiherenamasay	3–4	100	75	160	F	9		nd	IHSM
5	179	21.07.2001	Tsiandamba	5–6	>100	73	160	F	4	2	Jarifa	IHSM
6	205	18.05.2006	Nosy Lava	Nd	140	Nd	171	Nd			Nd	IHSM
7	231	18.02.2009	Fiherenamasay	Nd	200	nd	nd	nd			Jarifa	IHSM
8	232	July 2002	Toliara	nd	nd	35	150	nd			Jarifa	Not kept
9	244	20.09.2008	Cap Ste Marie	80	nd	40	150	nd			Jarifa	Copefrito
10	245	April 2008	Maintirano	nd	nd	nd	nd	nd			nd	Not kept
11	251	22-29.03.2001	Fiherenamasay	nd	120	80	180	F	2		Jarifa	IHSM
12	252	12.07.2005	Fiherenamasay	nd	nd	60.3	155	F	2		nd	Not kept
13	284	22-23.09.2010	W of Nosy Ve	>2	>150	85	187	F			Jarifa	IHSM
14	285	27.11.2010	W of Nosy Ve	1–2	250	41	134	M			nd	IHSM
15	310	April 2011	Onilahy Canyon	nd	>300	nd	nd	nd			nd	Not kept
16	288	5 May 2010	W of Nosy Ve	>1	150	nd	nd	F			Jarifa	Not kept
17	289	10.02.2011	W of Nosy Ve	20	200	80	175	F			Jarifa	IHSM
18	290	11.02.2011	W of Nosy Ve	2	200–300	60	149	F			Jarifa	IHSM
19	291	13.02.2011	NW Sarodrano	7	200–300	75	170	F			Jarifa	Copefrito
20	292	12.03.2011	NW Sarodrano	3	200–300	75.2	182	F			Jarifa	Copefrito
21	293	21.05.2011	W of Nosy Ve	2	150–200	29.45	130	M			Jarifa	Copefrito
22	294	02.07.2011	Andanora	7	150–200	84.64	170	F			Jarifa	Copefrito
23	295	03.08.2011	W of Nosy Ve	10	150–200	32	140	F			Jarifa	Murex
24	296	25.08.2011	W of Nosy Ve	2	150–200	62	170	F			Jarifa	Not kept
25	297	Jan 2012	St Augustin	nd	nd	nd	nd	nd			Jarifa	MHNH
26	311	31.05.2012	Fiherenamasay	nd	100–200	36	Nf	F			Jarifa	Not kept
27	298	July 2012	Toliara	nd	nd	nd	'Very large'	F			Jarifa	Not kept
28	312	2012	Maintirano	nd	100–200	36	nd	nd			nd	IHSM
29	301	Feb 2013	Ambanilia	6	500	35	130	M			Jarifa	Eden Ecolodge
30	313	Feb 2013	St Augustin	nd	nd	35–50	150	nd			nd	Not kept
31	314	2015	Anakao	nd	nd	nd	nd	nd			nd	Jardin de la Mer
32	315	11.06.2011	Toliara	nd	nd	nd	nd	nd			nd	DRAEP
33	316	23.03.2019	Barnhill Point	0.8–1	200	79	150	F			Jarifa	DRAEP
34	317	13.05.2010	W of Nosy Ve	nd	nd	nd	nd	nd			Jarifa	Not kept

Sources: Bruton and Coutouvidis[7], Nulens et al.[8], Heemstra et al.[11], Insacco et al.[12], Ravololoharinjara[23], Vicente[24], Niaina[25], Anon[26], Houssen[27] 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

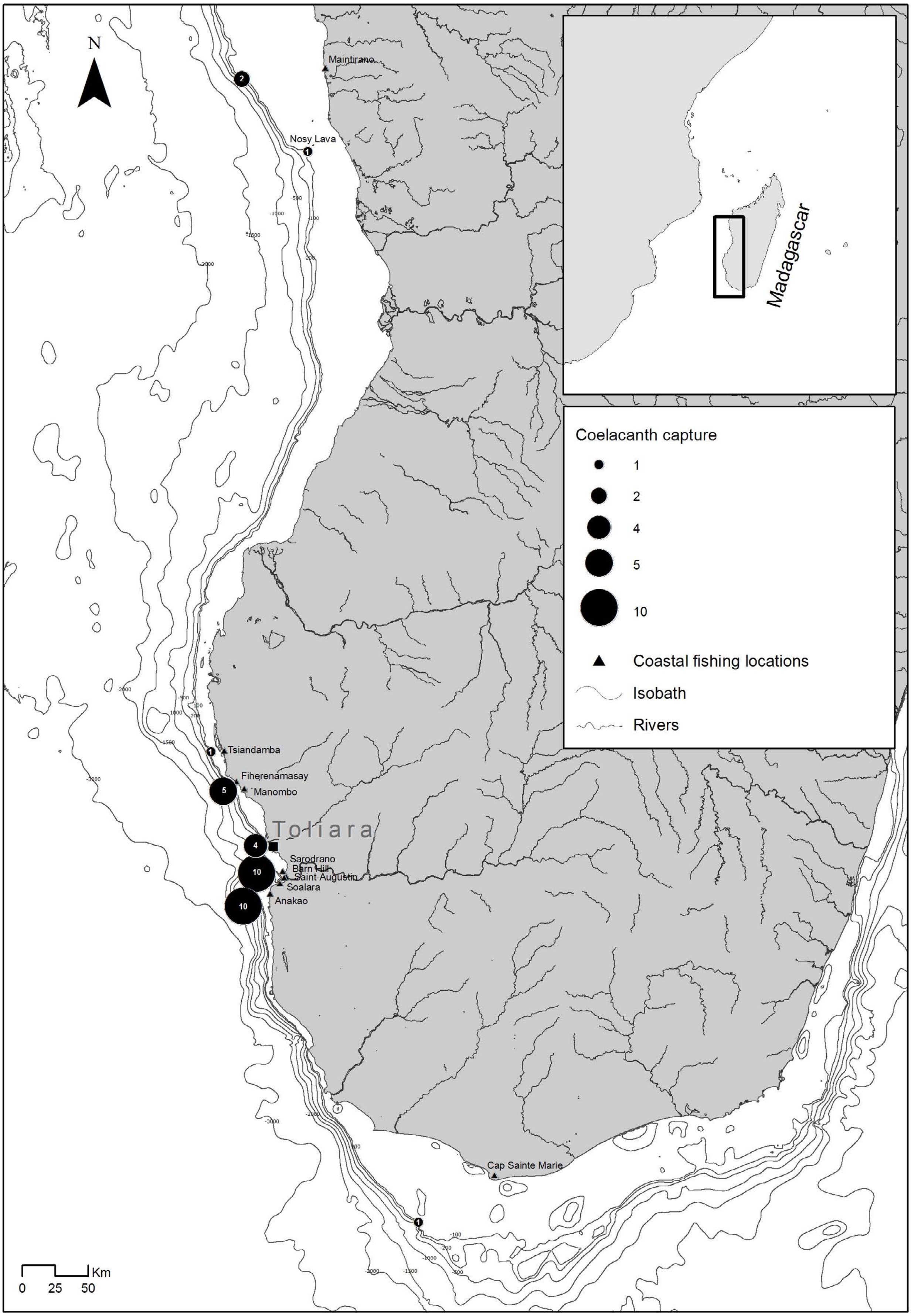

Figure 4: Map showing the location of captures from 1987 to 2019 of all coelacanths in Madagascar whose capture location is known.

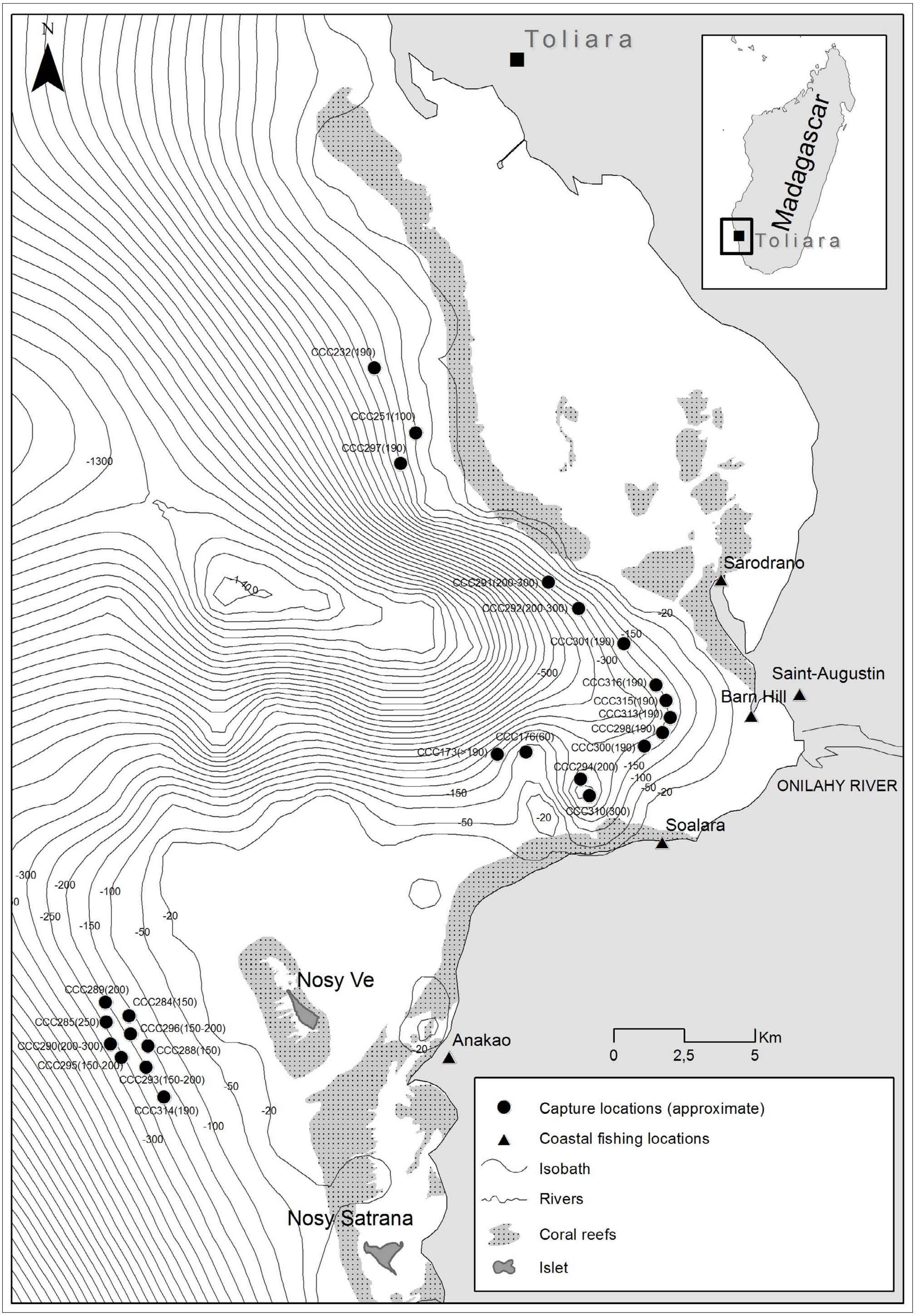

Figure 5: Map of St Augustin Bay, southwestern Madagascar showing the locations of the cluster of coelacanths caught from 1987 to 2019 near the Onilahy canyon.

Along the west coast, near the Onilahy canyon, the continental shelf is very narrow.[38] 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 *vezo* fishers regularly establish seasonal camps about 40 km offshore of the main island.[39] 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 (*galawas*). Handline fisheries, to which coelacanths are vulnerable, are therefore better developed in the Comoros than in Madagascar.[32,33,40]

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.[23] 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 2010[23] 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'[23]. He also reported to Ravololoharinjara[23] 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 March[8,33], whereas catches peaked in September (21%) and August (17%) in Tanzania[15]. All coelacanth captures in Madagascar for which the capture method is known (23) were made using deep-set *jarifa* gillnets targeting sharks[11,23] (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 parameters for female coelacanth catches in the Comoros[8,32,33], which reflects the higher proportion of females (which grow larger than males[8,40]) caught off Madagascar. The size of the 40 coelacanths caught off Tanzania (including Zanzibar) between 2003 and 2015 averaged 41.3 kg (range 5.8–105 kg) and 133.7 cm (range 70–184 cm), substantially smaller than the coelacanths caught off Madagascar, although the weight range is wider.[8,15] 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.[11,41]

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. Petit[42] found that shark fishing and shark fin exports from Madagascar were already established by 1900 and Schaeffer[43] 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.[30,44,45]

Shark meat is widely eaten by fishing communities in Zanzibar[43,46] and Madagascar[45], 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.[29]

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 'ZZ 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 nets[8] and, from the latter, 15-cm nets[15].

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 use[43], 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-reception[47], 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.[8,15,48]

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 (IHSM) has increased fishers' awareness of the coelacanth's significance and value. Baker-Médard and Faber[45] report payments of 150 000–400 000 ariary (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 Copefrito, 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 ariary per fish.[23] 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.

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.[5,32] 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.[20,47] 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.[48] *Jarifa* gillnets (in use or lost) are also known to catch dugongs and turtles in Madagascar.[49,50]

Outside Madagascar, the biggest threats to coelacanths, other than *jarifa* gillnets, are the use of explosives by fishers, recorded in Tanzania and the Comoros, and insecticide residues and plastic litter in the oceans.[8,15,51,52-55] 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 coelacanths store in their tissues like elasmobranchs, 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. Ravololoharinjara[23] was told that a 32-kg male fish (CCC 295) which had been housed in the cold room of the fishing company Murex in Toliara, had been 'shared with company personnel during the passage of Cyclone Haruna in 2013'. Coelacanth flesh is occasionally eaten in Tanzania[15] 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 Madagascar 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.[21] 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 P.C. Heemstra to the J.L.B. Smith Institute of Ichthyology (now South African Institute for Aquatic Biodiversity) in South Africa.[11] 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. mtDNA 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.[55]

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 Mozambique[13] and Kenya[14], 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[8,23], 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.[40]

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[5,56]) 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.[8,15] 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.[13] 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.[14] 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.[8,15] It is important to note that over 90% of all coelacanths larger than 50 kg are female[8,40] 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 Fricke et al.[52,54] 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 Mafuriko 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[5,15,48]).
- 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 v*ezo* 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 about 320 million years ago.[5] The survival of living coelacanths has therefore provided a unique window into the past. Their enormous 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.[5,52,57,58] 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.[5,52,57]

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.

References

1. Smith JLB. A living fish of Mesozoic type. Nature. 1939;143(3620):455–456. https://doi.org/10.1038/143455a0
2. Smith JLB. Old Fourlegs. The story of the coelacanth. London: Longmans, Green & Co.; 1956.
3. Bruton MN. The fishy Smiths. A biography of JLB and Margaret Smith. Cape Town: Penguin; 2017.
4. Smith JLB. The second coelacanth. Nature. 1953;171:99–101. https://doi.org/10.1038/171099a0
5. Bruton MN. The annotated Old Fourlegs. The updated story of the coelacanth. Cape Town: Struik; 2017.
6. Millot J. Le troisième coelacanthe [The third coelacanth]. Le Naturaliste Malgache, Premier Supplément 1954:1–26. French.
7. Bruton MN, Coutouvidis SE. An inventory of all known specimens of the coelacanth, *Latimeria chalumnae*, with comments on trends in the catches. Env Biol Fish. 1991;32:371–390. https://doi.org/10.1007/978-94-011-3194-0_25
8. Nulens R, Scott L, Herbin M. An updated inventory of all known specimens of the coelacanth, *Latimeria* spp. Smithiana Special Publication. 2011;3:1–52.
9. Millot J. First observations on a living coelacanth. Nature. 1955;175(4452):362–363. https://doi.org/10.1038/175362a0
10. Cloutier R, Forey PL. Diversity of extinct and living actinistian fishes (Sarcopterygii). Env Biol Fish. 1991;32:59–74. https://doi.org/10.1007/978-94-011-3194-0_4
11. Heemstra PH, Freeman ALJ, Yan Wong H, Hensley DA, Rabesandratana HD. First authentic capture of a coelacanth, *Latimeria chalumnae* (Pisces: Latimeriidae), off Madagascar. S Afr J Sci. 1996;92:150–151.
12. Insacco G, Nulens R, Zava B. The coelacanth, *Latimeria chalumnae* Smith, 1939 at the Natural History Museum of Comiso, taxidermic preservation and notes on the other world specimens. Natura Rerum. 2016;4(1):25–38.
13. Bruton MN, Cabral AJP, Fricke H. First capture of a coelacanth, *Latimeria chalumnae* (Pisces, Latimeriidae) off Mozambique. S Afr J Sci. 1992;88:225–227.
14. De Vos L, Oyugi D. First capture of a coelacanth, *Latimeria chalumnae* Smith, 1939 (Pisces: Latimeriidae) off Kenya. S Afr J Sci. 2002;98(7/8):345–347.
15. Benno B, Verheij E, Stapley J, Rumisha C, Ngatunga B, Abdallah A, et al. Coelacanth (*Latimeria chalumnae* Smith 1939) discoveries and conservation in Tanzania. S Afr J Sci. 2006;102(9–10):486–490.
16. Fraser MD, Henderson BAS, Carstens PB, Fraser AD, Henderson BG, Dukes MD, et al. Live coelacanth discovered of the KwaZulu-Natal south coast, South Africa. S Afr J Sci. 2020;116(3/4), Art. #7806. https://doi.org/10.17159/sajs.2020/7806
17. Pouyaud L, Wirjoatmodjo S, Rachmatika I, Tjakrawidjaja A, Hadiaty RK, Hadie W. Une nouvelle espèce de coelacanthe. Preuves génétiques et morphologiques. [A new species of coelacanth. Genetic and morphological evidence.]. Comptes Rendus des Sciences Naturelles. 1999;322(3):261–267. https://doi.org/10.1016/S0764-4469(99)80061-4 French.
18. Erdmann MV. An account of the first living coelacanth known to scientists from Indonesian waters. Env Biol Fish. 1999;54:439–443. https://doi.org/10.1023/A:1007584227315
19. Goodman SM, Benstead JP. Updated estimates of biotic diversity and endemism in Madagascar. Oryx. 2005;39(1):73–77. https://doi.org/10.1017/S0030605305000128
20. Fricke H, Hissmann K, Schauer J, Reinicke O, Kasang L, Plante R. Habitat and population size of the coelacanth *Latimeria chalumnae* at Grande Comore. Env Biol Fish. 1991;32:287–300. https://doi.org/10.1007/978-94-011-3194-0_20
21. Hissmann K, Fricke H, Schauer H, Ribbink AJ, Roberts MJ, Sink K, et al. The South African coelacanths – an account of what is known after three submersible expeditions. S Afr J Sci. 2006;102:491–500.
22. Green A, Uken R, Ramsay P, Leuci R, Perritt S. Potential sites for suitable coelacanth habitat using bathymetric data from the western Indian Ocean. S Afr J Sci. 2009;105(3/4):151–154. https://doi.org/10.4102/sajs.v105i3/4.68
23. Ravololoharinjara M. Rapport de Mission à Toliara pour l'inventaire des captures et spécimens de coelacanthes [Mission report to Toliara for the inventory of catches and specimens of coelacanths]. Resolve sarl internal report, November 2019. French.
24. Vicente N. Un coelacanthe à Madagascar [A coelacanth in Madagascar]. Océanorama. 1997;27:11–15. French.
25. Niaina N. A peine capturé un coelacanthe rejoint la marmite – capture d'un spécimen de coelacanthe au large de Maintirano [As soon as a coelacanth has been captured, it joins the cooking pot – capture of a specimen of coelacanth off Maintirano]. Les Nouvelles. 2006 July 01. French.
26. Anon. Le coelacanthe, icône de la Journée mondiale du Tourisme [The coelacanth, icon of World Tourism Day]. Les Nouvelles. 2005 October 05. French.
27. Houssen S. Le coelacanthe [The coelacanth]. Flaque et cours d'eau: Le journal du Collège Etienne de Flacourt, Tuléar, Madagascar. 2012;11 January 10. Available from: http://www.collegetulear.fr/fichiers_utiles/college_francais__journal_N11.pdf French.
28. Cooke AJ, Bruton MN, Ravololoharinjara M. Detailed table of coelacanths known to have been caught in Madagascar: 1987 to 2019 [document on the Internet]. [updated 2020 Sep 23; cited 2020 Oct 02]. Available from: https://www.resolve.mg/download/MadagascarCoelacanthInventory_23Sept2020.pdf
29. Cooke AJ. Survey of elasmobranch fisheries and trade in Madagascar. In: Marshall NT, Barnett R, editors. The trade in sharks and shark products in the Western Indian and Southern Indian and South East Atlantic Oceans. Nairobi: TRAFFIC East/Southern Africa; 1997. p. 101–130.
30. Cripps G, Harris A, Humber F, Harding S, Thomas T. A preliminary value chain analysis of shark fisheries in Madagascar. Unpublished report to the Indian Ocean Commission SF/2015/34; 2015.
31. Du Feu TA. Fisheries statistics for the large meshed gill net fishery, north west Madagascar. Internal report, Promotion de la Pêche Maritime Traditionnelle et Artisanale; September 1998.
32. Bruton MN, Stobbs RE. The ecology and conservation of the coelacanth *Latimeria chalumnae*. Env Biol Fish. 1991;32:313–339. https://doi.org/10.1007/BF00007464

33. Stobbs RE, Bruton MN. The fishery of the Comoros, with comments on its possible impact on coelacanth survival. Env Biol Fish. 1991;32:341–359. https://doi.org/10.1007/BF00007465

34. University of Berkeley. Where did all of Madagascar's species come from? Understanding evolution. Evo in the news. 2009 October. Available from: http://evolution.berkeley.edu/evolibrary/news/091001_madagascar

35. Ali JR, Aitchison J. Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth Sci Rev.* 2008;88:145–166. https://doi.org/10.1016/j.earscirev.2008.01.007

36. Ludt WB, Rocha LA. Shifting seas: The impacts of Pleistocene sea-level fluctuations on the evolution of tropical marine taxa. J Biogeogr. 2015;42:25–38. https://doi.org/10.1111/jbi.12416

37. Cooke AJ, Brand J. Madagascar – a guide to marine biodiversity. New York: Wildlife Conservation Society; 2012.

38. Battistini R, Jouannic C, Mauget LA, Castellato G, Vernier RE. Morphologie et sédimentologie du canyon sous-marin de l'Onilahy (S-W de Madagascar) [Morphology and sedimentology of the Onilahy submarine canyon (S-W of Madagascar)]. Cahiers de l'ORSTOM Série Géol II. 1975;2:95–110. French.

39. Cripps G, Gardner CJ. Human migration and marine protected areas: Insights from Vezo fishers in Madagascar. Geoforum. 2016;74:49–62. https://doi.org/10.1016/j.geoforum.2016.05.010

40. Bruton MN, Armstrong MJ. The demography of the coelacanth *Latimeria chalumnae*. Env Biol Fish. 1991;32:301–311. https://doi.org/10.1007/BF00007463

41. Schartl M, Hornung U, Hissmann K, Schauer J, Fricke H. Relatedness among East African coelacanths. Nature. 2005; 435:901. https://doi.org/10.1038/435901a

42. Petit C. L'industrie des pêches à Madagascar [The fishing industry in Madagascar]. Paris: Société d›éditions géographiques, maritimes et colonials, Bibliothèque de la faune des Colonies Françaises; 1930. French.

43. Schaeffer D. Assessment of the artisanal shark fishery and local shark fin trade on Unguja Island, Zanzibar. Independent Study Project (ISP) Collection. 2004;536:1–29.

44. Dockerty T. International trade in shark fins. Cambridge, UK: Wildlife Trade Monitoring Unit, World Conservation Monitoring Centre; 1992.

45. Baker-Médard M, Faber J. Fins and (mis)fortunes: Managing shark populations for sustainability and food sovereignty. Mar Policy. 2020(113);103–805. https://doi.org/10.1016/j.marpol.2019.103805

46. Barnett R. The shark trade in mainland Tanzania and Zanzibar. In: Marshall NT, Barnett R, editors. Trade review: The trade in sharks and shark products in the Western Indian and Southeast Atlantic Oceans. Nairobi: Traffic-East/Southern Africa; 1997.

47. Fricke H, Hissmann K. Feeding ecology and evolutionary survival of the living coelacanth *Latimeria chalumnae*. Mar Biol. 2000;136:379–386. https://doi.org/10.1007/s002270050697

48. Bruton MN. Traditional fishing methods of Africa. Cape Town: Cambridge University Press; 2017.

49. Kiszka JJ, Muir C, Poonian C, Cox T, Amir OA, Bourjea J, et al. Marine mammal bycatch in the Southwest Indian Ocean: Review and need for a comprehensive status assessment. West Indian Ocean J Mar Sci.2008;7(2):119–136.

50. Rakotonirina BP, Cooke A. Sea turtles of Madagascar – their status, exploitation and conservation. Oryx. 1994;28:51–61.

51. Bruton MN. When I was a fish. Tales of an ichthyologist. Cape Town: Jacana Media; 2015.

52. Fricke H. Die jagt nach dem Quastenflosser, der Fisch, der aus der Urzeit kam [The hunt for the coelacanth, the fish that came from prehistoric times]. Munich: Verlag CH Beck; 2007. German.

53. Hale RC, Greaves J, Gundersen JL, Mothershead II RF. Occurrence of organochlorine contaminants in tissues of the coelacanth *Latimeria chalumnae*. Env Biol Fish. 1991;32:361–367. https://doi.org/10.1007/BF00007466

54. Fricke H, Hissmann K, Schauer J, Plante R. Yet more danger for coelacanths. Nature. 1995;374:314. https://doi.org/10.1038/374314a0

55. Plon S, Thakur V, Parr L, Lavery SD. Phylogeography of the dugong (*Dugong dugon*) based on historical samples identifies vulnerable Indian Ocean populations. PLoS ONE. 2019;14(9), e0219350. https://doi.org/10.1371/journal.pone.0219350

56. Froese R, Palomares MLD. Growth, natural mortality, length-weight relationship, maximum length and length-at-first-maturity of the coelacanth, *Latimeria chalumnae*. Env Biol Fish. 2000; 58:45–52. https://doi.org/10.1023/A:1007602613607

57. Fricke H. Living coelacanths: Values, eco-ethics and human responsivity. Mar Ecol Prog Ser. 1997;161:1–15. https://doi.org/10.3354/meps161001

58. Cloutier R. Patterns, trends, and rates of evolution within the Actinistia. Env Biol Fish. 1991;32:23–58. https://doi.org/10.1007/BF00007444